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# **Factors Affecting the Identification of Phytoplankton Groups by Means of Remote Sensing**

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### **SUMMARY**

A literature review was conducted of the state of the art as to whether or not information about communities and populations of phytoplankton in aquatic environments can be derived by remote sensing. In order to arrive at this goal, the spectral characteristics of various types of phytoplankton were compared to determine first, whether there are characteristic differences in pigmentation among the types and second, whether such differences can be detected remotely. In addition to the literature review, an extensive, but not exhaustive, annotated bibliography of the literature that bears on these questions is included as an appendix since it constitutes a convenient resource for anyone wishing an overview of the field of ocean color.

The review found some progress has already been made in remote sensing of assemblages such as coccolithophorid blooms, mats of cyanobacteria, and red tides. Much more information about the composition of algal groups is potentially available by remote sensing particularly in water bodies having higher phytoplankton concentrations, but it will be necessary to develop the remote sensing techniques required for working in so-called Case 2 waters. It is also clear that none of the satellite sensors presently available or soon to be launched is ideal from the point of view of what we might wish to know; it would seem wise to pursue instruments with the planned characteristics of the Moderate Resolution Imaging Spectrometer-Tilt (MODIS-T) or Medium Resolution Imaging Spectrometer (MERIS).

## 1. INTRODUCTION

This report has as its major goal an assessment of whether or not information about communities and populations of phytoplankton in aquatic environments can be derived by remote sensing. In order to arrive at this goal, the spectral characteristics of various types of phytoplankton are compared to determine first, whether there are characteristic differences in pigmentation among the groups and second, whether such differences can be detected remotely. Mitchell and Kiefer have aptly stated an optimistic view to support such an effort. "...*in situ* or remote optical sensors may be capable of supplying information on algal physiology and ecosystem characterization including the extent of photoadaptation and the accumulation of small detrital particles derived from grazing." [1] A concurrent opinion comes from Millie and his colleagues: "High-resolution airborne remote sensing provides a means for monitoring local phytoplankton dynamics in temporal and spatial scales analogous to biotic and abiotic processes affecting such dynamics and necessary for applications to ecological research and fisheries or aquacultural management." [2]

Ocean color has proven to be a rich and dependable source of information on the abundance and distribution of phytoplankton, all of which contain chlorophyll *a*, the green pigment which is virtually the universal converter of light energy to chemical energy on earth. Chlorophyll *a* absorbs light particularly efficiently in the red and the blue portions of the spectrum. It is the absorption in the blue, when compared to absorption in the green, which is the basis for the quantitative detection of chlorophyll *a*. All phytoplankton - microalgae\* and cyanobacteria - have pigments in addition to chlorophyll *a* which modify or mask its green color. Thus these organisms may appear brown, yellow, blue-green, even red. Several researchers have pointed out the desirability of being able to remotely identify and quantify pigments in addition to chlorophyll *a*. Richardson and her associates, for instance, point out that the optical characteristics, i.e. the color, of the salt evaporation ponds which they were studying were determined by the biota, which consist of dense populations of algae and photosynthetic bacteria containing a wide variety of both photosynthetic and photoprotective pigments, and that the spectral signature of these pigments could be determined remotely. [3] In a similar situation, Millie's group used the Calibrated Airborne Multispectral Scanner aboard jet aircraft to provide reliable estimates of chlorophyll and carotenoid concentrations and phytoplankton standing crop in a series of finfish impoundments which varied dramatically. [2] The same is true of bodies of water in which the organisms are far more dispersed. Bidigare, with others, has been particularly active in elucidating the relationship between spectral irradiance in seawater and the phytoplankton pigments responsible, particularly of the chlorophylls. [4, 5]

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\*Algae refers to eukaryotic photosynthetic organisms, classified by some as Plantae, and by others as Protista. Until the last decade or so, photosynthetic bacteria containing chlorophyll *a* and evolving oxygen (cyanobacteria) were included in the term 'algae', being called "blue-green algae" or "cyanophytes". However, in recent years, the fact that cyanobacteria are prokaryotes, and clearly belonged in a different kingdom than any eukaryotic organism, has generally led to their exclusion from the term "algae". However, their role in the environment as primary producers, i.e. as reducers of carbon dioxide and evolvers of oxygen, makes it logical to include them functionally with the algae.

There are many examples of the potential value to biological oceanography of the ability to remotely sense photosynthetic pigments in addition to the ubiquitous chlorophyll *a*, and its degradation products; i.e., the other chlorophylls and the photosynthetically important carotenoids, as well as the phycobilins. Since the ensemble of pigments gives a mass of phytoplankton its characteristic color, it follows that the color can inform about the pigments present. The bluish green of chlorophyll *a* is often not obvious to the eye, but is masked by the other pigments which develop in aquatic organisms not only characteristic of a species, but also modified in response to the light environment and nutrition available. This report will show that there are pigments which may be correlated with particular groups of algae (often here referred to loosely as "taxa") or cyanobacteria, the eucaryotic algae and cyanobacteria being collectively termed "phytoplankton". It will also consider the potential for correlating such pigments with a spectral signature which might be detected remotely, thus indicating the presence of large numbers of a given group. As noted above, there are already preliminary indications that the potential is good, but still uncertain. Millie and Kirkpatrick have recently written: "Pigment signatures ...have been proposed to systematically differentiate between algal phylogenetic groups, and possibly between taxa. Advances in remote-sensing technology have lead to multi-spectral sensors capable of distinguishing spectral reflectance at sensitivities of 2 to 3 nanometers. However, whether these technologies used together can remotely characterize monotypic coastal assemblages remains unproven." [6] Individual cells are almost invariably too small to be seen with the naked eye, so enormous numbers must be present to effect a sensible impact on the color of the body of water in which they occur.

Some examples of oceanographic investigations which might benefit by the ability to identify the predominant algae by remote sensing follow. Malone and his associates investigated the mesoscale response of diatom populations to a wind event in the plume of the Hudson River. [7] A synoptic view which enabled them to determine what groups of phytoplankton were being affected by that event would have been of great value in augmenting their shipboard observations. Another example is provided by the work of Prezelin and her associates, who have not only determined that large differences in phytoplankton abundance and productivity occur across a thermal gradient, but that marked diurnal patterns also occur. In addition, they note that "The development of phytoplankton communities dominated by nano- and picoplankton-sized algae often are accompanied by a floristic shift from diatoms and dinoflagellates toward cyanobacteria and microflagellates" [8] - a shift which would be important to document with the synoptic view afforded by remote sensing of the characteristic pigments. A third example is provided by the work of Hoge and Swift who used LIDAR dual laser excitation to map chlorophyll *a* and phycoerythrin in a Gulf Stream Warm Core Ring; they showed a wide spatial variation in the distribution of the two pigments that could be linked to transition zones between coastal, Gulf Stream and Sargasso Sea water masses. [9]

The absorption spectrum of a population of photosynthetic micro-organisms in the laboratory or in the field is relatively straightforward to determine; however, the radiance (or reflectance) spectrum contains the information which can be detected remotely. These spectra are more difficult to determine, and direct measurements are less common. Richardson's group took advantage of the very concentrated populations in salt evaporation ponds to correlate absorption and radiance spectra with remotely-sensed data. [10][3] Arnone and his associates determined the upwelling and downwelling irradiances in small increments across the visible spectrum during a cruise which traversed strong frontal boundaries, correlating these with pigment concentrations determined analytically. [11] Bidigare's group measured photosynthetic pigments, nutrients, spectral irradiance and

various physical parameters, documenting the shifts in populations by direct microscopic observation. [12]

This report consists of a review of the current (1992) state of knowledge about pigments typical of taxa and their spectral signatures, and an extensive, but not exhaustive, annotated bibliography of literature that bears on these questions. While not every entry of the annotated bibliography will be cited in the text, the entire annotated bibliography is included as an appendix, since it constitutes a convenient resource for anyone wishing an overview of the field of ocean color. Many articles have to do with analyses of Coastal Zone Color Scanner (CZCS) images; some of them include information on the relationship between chlorophyll *a* and accessory pigments, or on the productivity of various groups of phytoplankton.

## 2. BACKGROUND

The Coastal Zone Color Scanner (CZCS), launched in October, 1978, was spectacularly successful in mapping the distribution of phytoplankton, based on a spectral signature characteristic of chlorophyll *a* which is ubiquitous in oxygenic photosynthetic organisms. Pure sea water appears to be blue due to molecular, or Rayleigh scattering, but chlorophyll *a* modifies the color of the light scattered out of the surface, shifting it towards green, because chlorophyll strongly absorbs blue light. While the synoptic images provided by the CZCS in eight years of operation number in the many thousands, and have been reproduced in innumerable articles, the atlas published at Goddard Space Flight Center titled "Nimbus-7 CZCS Coastal Zone Color Scanner Imagery for Selected Coastal Regions" contains a representative selection of these images together with text which explains the significance of the features observed. [13] It is not an exaggeration to assert that CZCS images have profoundly changed the field of oceanography, and that understanding of the dynamics of the world's oceans has been enormously strengthened by the synoptic view of those oceans over several years (1978-1986). As Morel and Berthon state, "The temporal and spatial requirements of global monitoring of marine photosynthesis can be met only by satellites, under the proviso that 'chlorophyll maps' produced from the data provided by ocean color sensors can be transformed into 'production maps'." [14]

## 3. CURRENT EFFORTS

Although the CZCS has not functioned for several years, the data collected are still being mined for information in two main areas. The main questions being asked are: first, what is the total amount of chlorophyll in a column of water; second, how does the chlorophyll content relate to the productivity, i.e. the fixation of CO<sub>2</sub>, of that water column. [15] These efforts will be briefly summarized below.

Other lines of investigation are being pursued in many laboratories which also bear on the questions posed for this study. The questions are: what accessory pigments (i.e. pigments other than chlorophyll *a*) occur in which taxa, and can these accessory pigments be used to uniquely identify species or other limited assemblages of phytoplankton? These, too, will be reviewed.

### 3.1 Estimates of total chlorophyll *a* from satellite (CZCS) data

The signal indicative of the presence of chlorophyll *a* which reaches the satellite sensors comes from the upper layers of the body of water. A great deal of effort has been devoted to the question of whether this signal can be related to the total amount of chlorophyll in the water column. A major problem is the fact that organisms, and hence chlorophyll *a*, are not uniformly distributed with depth. [16] Typically, there is a chlorophyll maximum considerably below the surface, where a large fraction of the photosynthetic organisms occur. However, the signal reaching the sensors of the satellite comes primarily from the upper layers. [17] The problem then becomes one of estimating the total chlorophyll from remotely sensed information which may not be representative of the whole column. [18] Such estimates may be valid in one area, but not in another. For instance, Hayward and Venrick have determined that surface chlorophyll may be closely correlated with the total integrated chlorophyll in the water column in the California Current and not at all in the central North Pacific. [19] If the emphasis is on estimating primary production rather than total chlorophyll, the deeper layers become less important because primary production depends on both chlorophyll concentration and available light.

While a detailed discussion of the question of the relationship of surface signal to total productivity is beyond the scope of this review, a few factors may be mentioned. Many environmental and physiological factors may govern the distribution of organisms. These include light intensity and spectral characteristics, nutrients, wind, season, and temperature. Different species of phytoplankton typically respond in different ways to the ensemble of factors in their environments. The chlorophyll maximum may occur at a depth which receives but a small percent of the light available at the surface. The amount of chlorophyll *a* per cell of a given species is not constant. This can change as a function of nutrient availability and the light regime, as discussed by Kiefer. [20] In addition, many areas of the ocean are not horizontally homogeneous with respect to phytoplankton distribution, but exhibit 'patchiness' which may or may not be within the resolution of the satellite detectors. [21, 22]

An additional factor complicating the estimation of total chlorophyll in a given column of water is evident from the work of Prezelin on "marine snow", which she defines as "a collective term for a variety of fragile, amorphous, macroscopic particles ranging from 0.5 mm to many centimeters in longest dimension". [23] Prezelin and her group have determined that in some cases, 29 to 249 times the abundance of several species of diatoms occur associated with these particles, compared with the abundance of the same species in an equal volume of water. Marine snow contained 74 times more Chl *a* and 127 times more phaeopigments than an equal volume of surrounding seawater. However, equivalent determinations made two weeks later yielded very different results, being far less productive. [23]

Despite these factors which contribute to the difficulty and uncertainty of estimating total chlorophyll from the remote signal, reports from several labs indicate that fairly good estimates of total chlorophyll and productivity may be derived from CZCS data. Balch and his associates used pigment and temperature values for describing maximum photosynthesis in surface waters in the southern California Bight. From these, they devised a model for the vertical distribution of chlorophyll which simplified the estimation of those pigments too deep for the satellite to detect. [18, 24]

Carder and his associates found good agreement between satellite-derived and shipboard measurements of chlorophyll *a* and phaeophytin *a* [25] while Eppley's group noted that the proportionality factor, *F*, between chlorophyll concentration and primary production varied as a function of changes in insolation, but even more to changes in the depth of mixing. [17, 26] Morel and Berthon found that "highly significant relationships were found (between actual concentration of pigments in a vertical profile and mean concentration in the euphotic layer) allowing the pigment content of the euphotic layer to be inferred from the surface concentration observed within the layer of one penetration depth." [14] Mueller *et al.* warn that the algorithms are reliable only in open ocean waters. [27] Platt and Herman are sanguine in noting that although "Remotely-sensed data contain only a small (5 percent of biomass and 11 percent of the turnover) but surprisingly stable fraction of the information in the water column [16], while Sathyendranath and Platt show that if the shape of the (vertical) pigment profile is known from independent data, the entire pigment profile may be recovered from the satellite data...". [28] And finally, Smith and his associates state that "Recent advances in remote sensing of ocean color have made synoptic estimation of phytoplankton biomass attainable." but caution that "rapid shipboard estimates of the vertical distribution of primary productivity, on mesoscale spatial scales and event-time scales are needed to provide both surface validation and data for the development of bio-optical models linking production to the optical characteristics of the water column." [29, 30]

Balch notes that the satellite underestimated the true pigment concentration in mesotrophic and oligotrophic waters ( $< 1 \text{ mg pigment m}^{-3}$ ) and overestimated the pigment concentration in eutrophic water ( $> 1 \text{ mg pigment m}^{-3}$ ). [31] A report by Banse and McClain on winter blooms in the Arabian Sea confirms this generalization. [32]. Mitchell, working with data from polar oceans, also has concluded that the presently recommended water-leaving radiance algorithm for CZCS data processing underestimates surface pigment concentrations by more than a factor of two for polar observations. [33]

Many attempts are being made to derive bio-optical algorithms which will give improved accuracy of the estimates of total chlorophyll derived from a satellite. [18, 34] Balch has recently compared these, and notes that elaborate models do no better than simple, three parameter models in integrating primary production, mainly due to lack of knowledge about the photoadaptive parameters in space and time. [24] Carder and his associates found good agreement between satellite-derived and shipboard measurements of chlorophyll *a* and phaeophytin *a* concentrations despite contributions from non-living particles and non-water (Gelbstoff) components, since all of these increase with chlorophyll. [25] However, remote-sensing algorithms should be developed that respond to regional conditions [35], since the population of light-absorbing particles in the ocean includes many types in addition to phytoplankton. [36] Techniques for partitioning and quantifying these several contributions is beyond the scope of this review, but the fact that they exist should not be lost sight of in evaluating information derived from ocean optical properties. Some additional comments about Gelbstoff are in Section 8.

### 3.2 Estimates of primary productivity from satellite data

Estimates of productivity are derived from the distribution and concentrations of chlorophyll in the oceans as detected by its optical signal reaching the satellite. "Satellites provide the only avenue by which marine primary production can be studied at ocean-basin scales." [37]

The amount of chlorophyll in the water must be converted to carbon dioxide fixation in the entire water column. "The step of converting surface pigment data to integral production data has admittedly been difficult due to several factors such as limited depth of the phytoplankton visible to the satellite, variable fraction of phaeopigments versus chlorophyll, variable phytoplankton species and varying physiology" [31]

Collins' group has made estimates of oceanic primary production on a global scale, using only satellite data, i.e. the CZCS with the addition of surface temperature (AVHRR) and a determination of the incident solar irradiance responses of phytoplankton to differing light and nutrient fields. [38] Morel and Berthon, in an important paper, assert that "...we can compute primary production from ocean color data acquired from space." They state that "The temporal and spatial requirements of global monitoring of marine photosynthesis can be met only by satellites, under the proviso that 'chlorophyll maps' produced from the data provided by ocean color sensors can be transformed into 'production maps'." [14]

Given an estimate of the total chlorophyll underlying some unit of surface area of the ocean, the problem becomes one of relating that instantaneous chlorophyll concentration to the amount of carbon dioxide fixed in a unit of time - day, season, or year. A number of assumptions must be made. The amount of  $\text{CO}_2$  fixed is a function of the amount of light the organism receives, its nutrition, diurnal pattern, and its temperature. [39] Moreover, spectral quality has a marked effect on both pigmentation and quantum yield. [40] Thus even for a population made up entirely of a single species, there is potentially a range of rates of fixation per cell per unit time. However, these variables can be modeled, or directly determined by sampling. The surface temperature can be determined remotely, and the light at a range of depths modeled. The nutrients available must be measured directly, or inferred.

The species of phytoplankton is also an important variable in converting a given concentration of chlorophyll *a* to productivity. Laboratory data for unialgal cultures can be used as the basis for estimating the efficiency (or relative efficiency) of different species in fixing carbon dioxide. While each major group of algae contains many species which may well comprise a wide range of efficiencies, it is nevertheless probably valid to assign a 'typical' rate to the group, or a range of rates relative to other groups, even though the distribution of species is not uniform with depth. [12, 41] This fact provides one of the the most important rationales for trying to determine which type of algae predominates in any area for which the productivity is to be estimated.

Despite the factors which may contribute to uncertainties in remote determination of pigments, and the consequent ability to estimate global productivity, the effort to derive productivity data from satellite data is extremely important from the viewpoint of a global ecology [42] and considerable progress has been made towards this goal. [43]

#### 4. BEYOND THE COASTAL ZONE COLOR SCANNER AND CHLOROPHYLL A : CAN ALGAL GROUPS BE IDENTIFIED REMOTELY BY THEIR SPECTRAL SIGNATURE?

Phytoplankton derive their color from the relative proportions of various pigments, which fall into three classes; the chlorophylls and the carotenoids which are both lipids, and the phycobilins, which are water soluble. Absorption spectra have long been the preferred mode of visualizing the properties of pigments. Figure 1 shows the *in vivo* absorption spectra of representative photosynthetic species. The alpha peak of chlorophyll *a* at approximately 680 nm *in vivo* is prominent in all the oxygen-evolving photosynthetic organisms. (B through F in Figure 1). Note that B, *Anacystis*, is representative of the cyanobacteria, while C-F are all eucaryotes. The photosynthetic bacteria (e.g. *Rhodospirillum rubrum*) which are anaerobes, possess forms of chlorophyll whose main absorption peak is shifted towards the red. However, these organisms contribute little to the ocean's productivity, although they may play an ecologically important role in some lakes.

The lipid pigments fall into two main classes: the chlorophylls (*a*, *b*, *c1*, *c2*, *c3*) which are tetrapyrroles and their degradation products, and the carotenoids: carotene and a large number of oxidized carotene derivatives, collectively called the xanthophylls. All except chlorophyll *a* are termed accessory pigments. Figure 2 shows the *in vitro* absorption spectra of the pigments in photosynthetic organisms.

The chlorophylls function as light-gatherers, and pass light excitation to reaction centers consisting of chlorophyll *a* in a specialized environment. Note that each of the chlorophylls has a pair of prominent peaks, one in the red end of the spectrum, (the alpha peak) the other in the blue (the Soret band). Since water absorbs red strongly, the blue peak is most useful for remote sensing, which depends on the signal provided by light scattered out of the water column. [44-46] This consideration prompted the choice of bands in the CZCS which was designed to detect chlorophyll *a* only. While the alpha peak of chlorophyll *a* has a maximum at approximately 680 nm, when chlorophyll *a* is extracted into acetone, the peaks are shifted towards the blue, with the alpha peak of chlorophyll *a* typically at 663 nm in the extract. Chlorophylls *b*, *c1*, *c2*, and *c3* are accessory pigments which function as light gatherers only; the sole energy converter is chlorophyll *a*.

The carotenoids can function as light gatherers or as photoprotective agents. The distinction is important if one is interested in the fluorescent properties of the algae, since only the pigments which are photosynthetically active can give rise to a fluorescence signal. [47] While some carotenoids are ubiquitous (e.g. beta carotene), some are essentially diagnostic of given groups. For example, peridinin, described as "mahogany red" only occurs in dinoflagellates [47], and fucoxanthin is confined to the diatoms and chrysophytes. [48] All the carotenoids absorb strongly in the blue end of the spectrum, and largely overlap (see Figure 2).



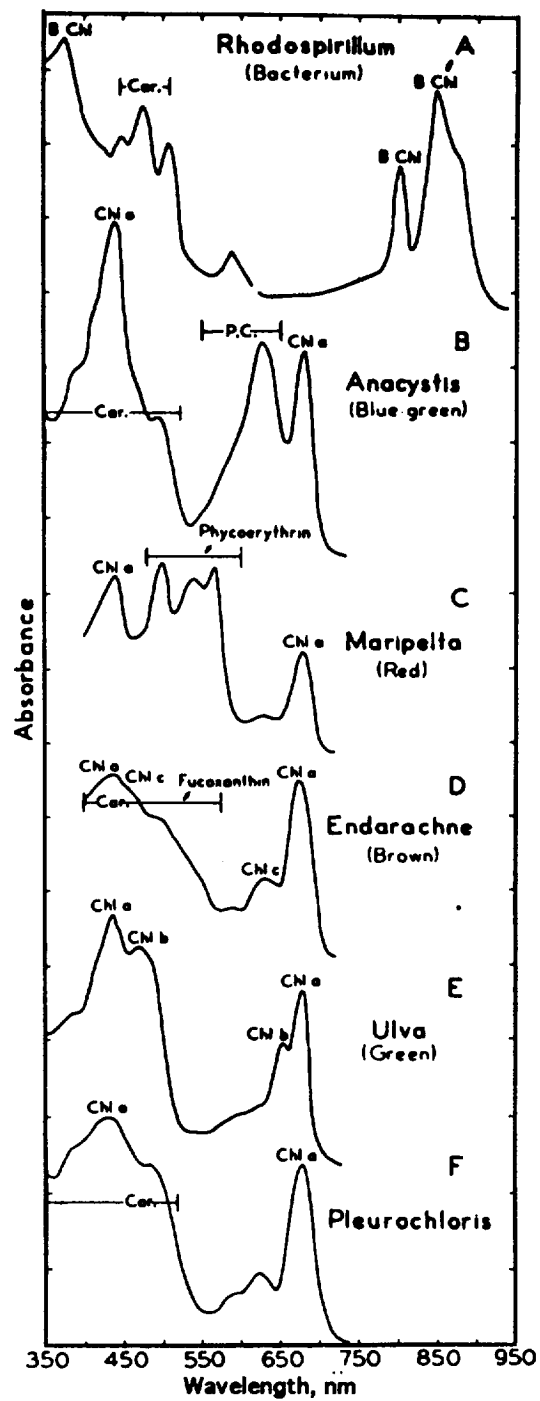
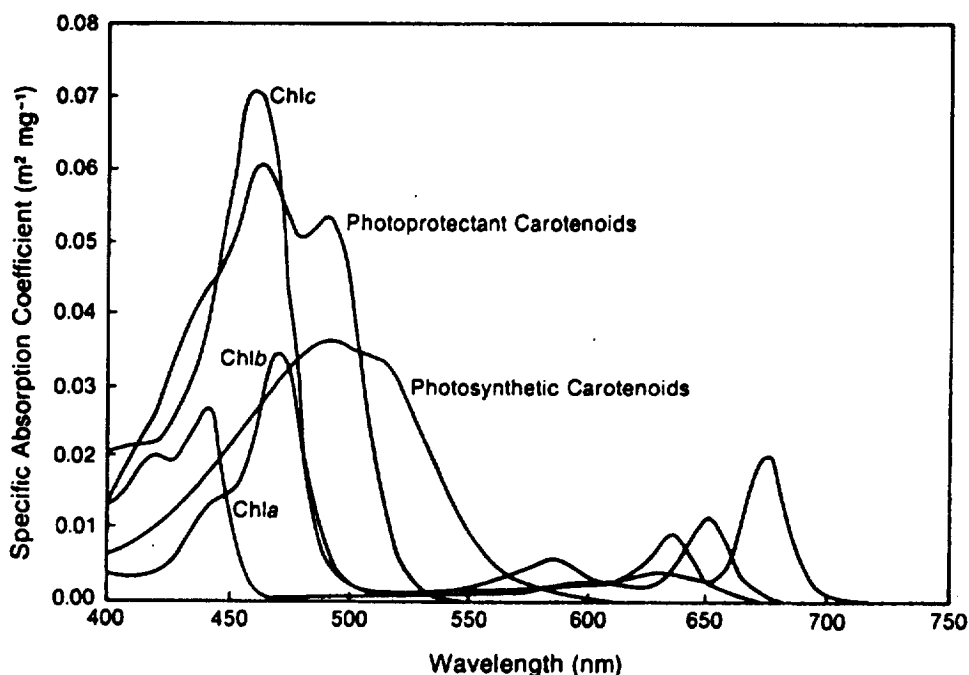


Figure 1. *In vivo* spectra of representative photosynthetic organisms. (from Prezulin and Boczar, 1986) [48]

The biliproteins (or phycobilins) constitute a third class of pigments which function as the accessory pigments of the cyanobacteria and red algae (of which there are only a small number of unicellular forms). These are water-soluble, and at present no HPLC technique for separation and quantification of these pigments exists. [49] Indeed, there is no satisfactory, widely-used technique for their analysis which is comparable to HPLC. The phycobilins can be effectively extracted with 50% glycerol; lysozyme enhances the efficiency of extraction. [49] Phycobilins are highly fluorescent, and accurate quantification on a per cell basis is possible with flow cytometry. [49] Figure 3 shows the absorption spectra of the biliproteins from cyanobacteria.



**Figure 2.** *In vitro* spectra of pigments in photosynthetic organisms. (from Bidigare *et al.*, 1990) [12]

The pigments which set the cyanobacteria aside from most eucaryotic algae have taken on increased importance with relatively recent discoveries about the role of cyanobacteria in the world's aquatic ecosystems. Cyanobacteria are now known to fix a substantial portion of the oceanic carbon dioxide; they had evaded detection earlier because of their small size. Relatively recently it has been discovered that very small phytoplankton cells ("picoplankton"), characterized as less than 1  $\mu\text{m}$  in diameter, make a substantial contribution to the ocean's productivity. This contribution is 20 to 80 percent of the inorganic carbon fixation. Because of their small size, they pass through the filters routinely used to collect particulate matter in water samples. [50] [51] However, it should be noted that picoplankton probably consist of both cyanobacteria, with their characteristic phycobilins, and eukaryotic cells, which mostly lack these pigments. [52] [53]

On a different scale, large floating masses of a filamentous form of cyanobacteria, *Trichodesmium*, (also known as *Oscillatoria*) are of enormous importance in fixing dinitrogen and thus infusing new combined nitrogen into the oceans. Indeed, Paerl tells us that "From a biogeochemical perspective, the degree to which dinitrogen fixation can supply nitrogen requirements plays a key role in determining the trophic state and fertility in individual aquatic environments, regardless of salinity." [54] Since primary production in aquatic ecosystems is often limited by the supply of combined nitrogen, a method of assessing the worldwide distribution of *Trichodesmium* should be a priority in designing future detectors for remote sensing. While Subramanian reports that he can detect floating mats of *Trichodesmium* in CZCS images of the Indian Ocean ([55] and personal communication) by using band 3 (550 nm) associated with chlorophyll, relatively little attention has been paid to this potential for remote sensing.

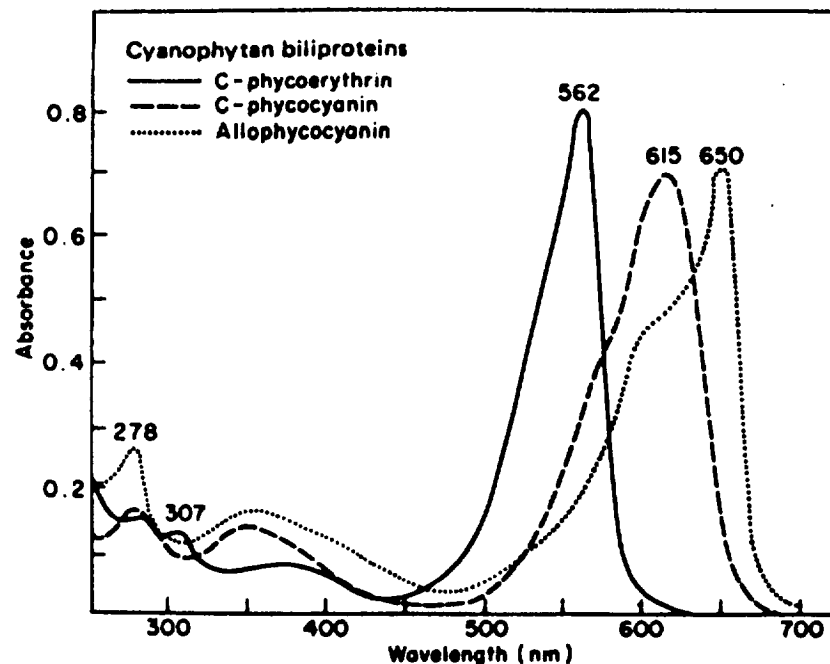


Figure 3. Biliproteins from pure cultures of cyanobacteria: C-phycoerythrin from *Phormidium persicinum* (solid line), C-phycocyanin from *Nostoc muscorum* (broken line), allophycocyanin from *Nostoc muscorum* (dotted line). (From Prezelin and Boczar, 1986.) [48]

Lewis and his associates report on the photosynthetic action, absorption and quantum yield properties of these important organisms. While the absorption spectrum is generally characteristic of cyanobacteria, there is a prominent peak at 493 nm, characteristic of phycourobilin, along with smaller peaks at 627 and 567 nm. [56] (Note that these peaks are not included in Figure 3.)

Moreover, cyanobacteria can constitute "nuisance blooms", particularly in fresh water habitats, and are of particular interest for this reason. Paerl and his associates have been studying massive blooms of the cyanobacterial nuisance genera *Anabaena*, *Aphanizomenon*, and *Microcystis* in previously bloom-free North Carolina rivers and estuaries. [54, 57] They urge immediate attention to these potentially ecologically and economically devastating phytoplankton blooms. Sakshaug and his group also make a strong case for using remote

sensing to detect those pigments characteristic of toxic blooms. [47] For instance, Prymnesiophytes can form blooms of toxic species which are harmful to fish and bottom fauna; these have not only chlorophyll *c*3, but also fucoxanthin and the carotenoid 19'hexanoyloxy-fucoxanthin, which causes a characteristic shoulder at 470 nm in the absorption spectrum. Timely detection by remote sensing of the characteristic cyanobacterial pigments would help alert those who are concerned with the combination of factors responsible for their appearance.

Finally, a novel class of photosynthetic organisms, the Prochlorophytes, was first reported by Chisholm and her associates in 1988. [58] These are very small prokaryotes, barely visible in the light microscope, but extremely abundant (up to  $10^5$  cells per ml.) in the deep euphotic zone. They contain chlorophyll *b*, but lack the phycobilins characteristic of cyanobacteria, so their pigmentation generally resembles that of the Chlorophytes and other green plants in including chlorophyll *b*. However, the chlorophyll *a* is a divinyl form with the Soret band shifted 8-10 nm to the red of the normal form. [58] This combination of pigments would appear to be sufficiently novel to potentially be able to map them by remote sensing, provided they were sufficiently abundant within the layers accessible to detection.

Prezelin and Boczar have provided an excellent review on the molecular bases of cell absorption and fluorescence in phytoplankton, with their potential applications to studies in optical oceanography. [48] From their work, as well as that of others, it is clear that the pigments in phytoplankton contain an enormous amount of information in their absorption and fluorescence characteristics which is sure to enrich the understanding of aquatic ecosystems, by providing insights into the environmental factors regulating photosynthetic efficiencies in surface waters of the world's oceans. The challenge lies not only in detecting these signals, but in their interpretation. The remotely-sensed signal must always be related to valid ground-truth data.

## 5. ANALYSIS OF ALGAL PIGMENTS

As has been discussed above, pigmentation does characterize certain groups of phytoplankton. Absorption spectra of the organisms and their extracts have long been the chief means of pigment identification and quantification; however, minor components may be difficult to identify and quantify unambiguously from absorption spectra, as they may be swamped by the major components.

Chromatography separates pigments into discrete bands; thin layer chromatography can furnish detailed data on identities and quantities of pigments in the hands of skilled persons such as Jeffrey and her associates. One of Jeffrey's telling observations links the variety of algal pigments to their habitats; whereas terrestrial plants have evolved only one light-harvesting system, algae must be adapted to utilizing particular wavelengths of the full visible spectrum, usually at light intensities much reduced from those at the sea's surface. [59, 60] As a consequence, phytoplankton have evolved a great variety of pigment systems. However, pigments must be quantitatively analysed. High Performance Liquid Chromatography (HPLC), has recently come into widespread use for its application to pigment analyses. It is currently the analytical method of choice, revealing a wealth of information heretofore unsuspected.

HPLC methods suitable for examining phytoplankton pigments, which include the carotenoids as well as the chlorophylls have been published by Wright's group. Their 1991 paper includes chromatograms from 12 unialgal cultures from 10 algal classes, separating over 50 carotenoids, chlorophylls and their derivatives. [61] Others have also analyzed pure cultures of algae for their pigment content. For example, 16 coccoid eukaryotic ultraplanktonic clones isolated from both coastal and oceanic water revealed four different HPLC signatures. [53] The HPLC technique has been extended to pure cultures of photosynthetic bacteria [62].

Similar analyses have been made of natural assemblages, usually validated by microscopic determination of the species present. For instance, Tester and Geesey sampled two sites twice weekly in the Newport estuary. They determined phytoplankton species composition, cell numbers, chlorophyll *a* and HPLC pigment analyses for each of 52 samples over four months. Fluctuations of phytoplankton species composition in the shallow, upper estuary site were closely correlated with wind and storm events, while in the lower estuary they were correlated with temperature. They noted a strong correlation between peridinin and the number of dinoflagellates, while chlorophyll *a* was a poor predictor of the numbers of dinoflagellates. [63] Ondrusek and his associates report on the distribution of phytoplankton pigments in the North Pacific Ocean in relation to physical and optical variability. [64] Wright and his colleagues isolated 50 different chlorophylls, carotenoids and their degradation products from marine phytoplankton using HPLC [61], whereas Cleveland *et al.* did a particularly thorough job of applying and correlating various techniques including HPLC on a Biowatt cruise to the Sargasso Sea in 1987. [36]

Many researchers have published both methods and findings. Bidigare has described a shipboard HPLC system which can provide quantitative determinations of chlorophylls *a, b, c*, and their degradation products. The method is fast (<20 minutes), precise, and can detect chlorophyll *a* concentrations as low as 13 pg per injection. He and his colleagues have demonstrated its usefulness in a number of oceanographic investigations. [36, 65, 68] Everitt and his colleagues examined phytoplankton community compositions from 11 locations in the western equatorial Pacific by using HPLC to identify seven different carotenoids and to determine the chlorophyll/pigment ratios. These data allowed them to determine the composition (by class) of the phytoplankton communities. However, they warn that the use of pigments as algal markers depends on how specific a given pigment is for a given group; some marker pigments are not present in all species within an algal class. For instance, only peridin-containing dinoflagellates can be recognized; heterotrophs, fucoxanthin-containing species or those having endosymbiotic chrysophytes or cyanobacteria are not detected by this method. Zeaxanthin, formerly thought to be present only in cyanobacteria, is also present in recently-discovered prochlorophytes; chlorophyll *b*, formerly thought to be confined to chlorophytes, also occurs in prochlorophytes. [66] Others have used HPLC to probe such phenomena as brown tides [67], red tides caused by *Gymnodinium breve* [6], the vertical partitioning of pigments [64], or the algae responsible for the production of dimethyl sulfide. [69]

A report of a recent workshop on evaluating and comparing spectrophotometric, fluorometric and HPLC methods for algal pigment determinations is especially useful. In addition, the relationships between algal spectral reflectance signatures, pigment absorbance spectra, and HPLC are discussed. [49] It is clear that a number of algal groups can be characterized by the presence of certain pigments. Table 1 is adapted from Paerl and Millie (1991) and lists major phytoplankton pigment groups (chlorophylls, carotenoids, phycobilins) useful as diagnostic taxonomic and physiological markers. [49] However, Paerl and Millie,

reporting on a conference, caution as follows: "Presently, identification of algal systematic groupings through pigment signatures appears to be limited to the division level. Distinction beyond this phylogenetic classification should be made with caution. For example, within the green algae, the presence or absence of select carotenoids has been included for class or order distinctions. However, HPLC pigment analyses have indicated that the distributions of several of these carotenoids are disjunct and do not have apparent systematic utility." [49]

While the presence or absence of marker pigments has been used for some years to provide qualitative descriptions of phytoplankton communities, only recently have there been attempts to estimate the contributions of various algal groups to total biomass from the proportions of marker pigments. Everitt and his colleagues have used the approach that certain chlorophyll *a*/marker pigment ratios are characteristic of each of the algal groups. They then calculate the relative proportions of each algal class in the phytoplankton biomass and community structure. [66] Table 2 is adapted from Everitt *et al.* (1990) in which the ratios of certain pigments are indicative of specific classes.

HPLC is being used on shipboard for the rapid determination of chlorophylls and their degradation products. Its usefulness for this purpose has been demonstrated along two long-line transects in the Southern Ocean, in which over 500 suspended particulate samples were analyzed for porphyrin content. Although variations were noted, overall chlorophyll *a* accounted for approximately half of the pigments measured; the dominant accessory and degraded porphyrins were chlorophyll *c* and phaeophorbide *a*, respectively. [68]

In addition to eukaryotic chlorophylls, bacteriochlorophylls can also be detected, identified and quantified by HPLC. Heretofore, there had been no widely accepted, standard assay for individual bacteriochlorophylls in field samples, "even though phototrophic bacteria can dominate anoxic regions of the water column, exerting a significant influence on primary production, elemental cycling, and trophic interactions." [62] Hurley and Watras have determined the HPLC and absorption spectra of five bacteriochlorophylls from pure cultures. Their application of this information to lakes in northern Wisconsin indicated that phototrophic bacteria may be more widespread than had been thought. Moreover, their presence gives evidence of the environmental conditions controlling their growth, since pH, sulfur or sulfide, light field, oxygen tension are all significant variables. Finally, this important paper points out that in the past some pheophytins have been confused with bacteriochlorophylls, and describes methods for their unambiguous separation. They caution: "Without HPLC separation, misidentification of pigments is likely and can lead to serious misinterpretation of planktonic distributions and processes." [62] Shapiro's group has compared immunological signatures of marine coccoid ultraplankton (< 3  $\mu$ m) with their HPLC signatures and found concordance in the affinities determined by these two methods. [70] HPLC has indeed become an essential tool in investigating oceanic and estuarine as well as lake processes.

**Table 1. Major phytoplankton pigment groups useful as diagnostic taxonomic/physiological markers. (Adapted from Paerl and Millie, 1991) [49]**

Pigment	Use
<u><b>Chlorophylls</b></u>	
Chlorophyll <i>a</i>	sole chlorophyll in cyanobacteria; in proportion to Chls. <i>b</i> and <i>c</i> in other groups.
Chlorophyll <i>b</i>	only present in chlorophytes
Chlorophyll <i>c1</i>	present in chrysophytes and diatoms
Chlorophyll <i>c2</i>	present in dinoflagellates, cryptophytes, and certain diatoms
<u><b>Carotenoids</b></u>	
Echinenone	cyanobacteria
Aphanaxanthin	cyanobacteria
Nostoxanthin	cyanobacteria
Myxoxanthophyll	cyanobacteria
Zeaxanthin	cyanobacteria , prochlorophytes [66]
Neoxanthin	euglenophytes
Peridinin	dinoflagellates
Alloxanthin	cryptophytes
Prasinoxanthin	prasinophytes
Lutein	chlorophytes
19'-butanoyl-fucoxanthin	chrysophytes
Fucoxanthin	prymnesiophytes, diatoms
Beta-carotene	in all groups, in varying proportions
<u><b>Phycobilins</b></u>	
Allophycocyanin	cyanobacteria
Phycocyanin	cyanobacteria
Phycoerythrin	cyanobacteria

**Table 2. Marker pigment ratios used to estimate the contribution of phytoplankton classes to chlorophyll *a*. (Adapted from Everitt *et al.*, 1990) [66]**

Class	Pigment ratio	Iterated values
Dinoflagellates	Chl <i>a</i> /peridinin	2.58
Cryptomonads	Chl <i>a</i> /alloxanthin	2.01
	beta carotene/alloxanthin	0.34
Prasinophytes	Chl <i>a</i> /prasinoxanthin	4.2
	Chl <i>b</i> /prasinoxanthin	2.08
Other greens	Chl <i>a</i> /Chl <i>b</i>	0.75
	zeaxanthin/Chl <i>b</i>	0.019
Prochlorophytes	Chl <i>a</i> /beta carotene	4.86
	Chl <i>b</i> /beta carotene	7.97
	Chl <i>b</i> /Chl <i>a</i>	0.93
	zeaxanthin/Chl <i>b</i>	0.16
Cyanobacteria	Chl <i>a</i> /zeaxanthin	1.7
Prymnesiophytes	Chl <i>a</i> / butanoylfucoxanthin	1.6
	fucoxanthin/butanoylfucoxanthin	0.084
Diatoms	Chl <i>a</i> /fucoxanthin	1.4

(The iterated values were derived from seed values taken from the literature, and adjusted according to a complex procedure to best reflect the reality of the conditions being measured. [66])

The widespread application of HPLC in a variety of contexts has led to the realization that there are many more carotenoids than had heretofore been suspected. The text by Goodwin, *The Biochemistry of Carotenoids*, especially the chapter on the algae [71], remains a valuable and encyclopedic reference for structure and spectra of carotenoids.

Nelson and his associates have determined the influence of the 'package effect' on phytoplankton absorption spectra. [72] (The 'package effect' refers to the fact that because pigments are localized on membranes within cells, the arrangement of these membranes can lead to differing internal absorption and scattering, depending on the shape and size of the cells. This results in differing external optical characteristics for equal amounts of pigments. Large, densely-packed cells exhibit decreased absorption efficiency compared to small cells with less concentrated pigments.) They compared absorption spectra made from direct measurements with spectral reconstructions calculated from HPLC-determined pigment concentrations. Working in a hydrographically variable region of the Southern California Bight, they found measurable packaging effects in fewer than 25% of their samples, principally those taken in the subsurface chlorophyll maximum layer and in association with populations of large diatoms or dense prymnesiophyte concentrations. When packaging effects were significant, they could be corrected for by measuring phytoplankton absorption at 675 nm and applying an appropriate algorithm. [72]

Pigmentation is not necessarily a fixed property of a species. The quantity and quality and proportions of pigments may vary with amount and spectral quality of light, with



nutritional status, and with age of the culture. Thus an ensemble of spectra might all be characteristic of a single group of algae under differing environmental or physiological conditions. [11, 73] However, even with these difficulties, certain characteristic colors are typical of certain types of algae in both fresh and salt water environments.

## 6. CAN ACCESSORY PIGMENTS BE DETECTED BY BACKSCATTERED LIGHT?

The answer is a qualified "yes" which represents the consensus of those working actively in the field. This answer implies that major groups of phytoplankton can be distinguished remotely.

While there are few measurements of surface reflectance in conjunction with *in situ* analysis of pigments and species, Richardson (with her associates) has shown in her studies at hypersaline ponds in Guerro Negro, Mexico, that reflectance at 620 nm (the specific absorbance peak of the cyanobacterial pigment phycocyanin) agreed with digital data from a Landsat Thematic Mapper satellite image of the study area. Unfortunately, the next satellite to target ocean color, SeaWiFS, has no band at 620 nm. [3, 10]

Robert Bidigare is optimistic about using accessory pigments for detecting major algal groups. He is working with C. Davis and T. Carter, measuring upwelled radiation at about 10 wavelengths, and is also trying to do derivative spectrometry. (Personal communication) Bidigare notes that there is far more diversity of pigments than had been realized just a few years ago. For instance, there are at least 5 different chlorophylls; besides *a* and *b*, there is a whole suite of chlorophyll *c*'s, which differ in their absorption in the blue by 5-8 nanometers. Blooms of *Phaeocystis* have chlorophyll *c3*; in diatoms, chlorophylls *c1* and *c2* are both present. In Prymnesiophytes, chlorophyll *c2* dominates. The red tide dinoflagellates are dominated by *c3*. On the other hand, Raymond Smith said he was pessimistic about using the carotenoids to sort out algal groups by remote sensing, since the carotenoid spectra are all similar (personal communication). (See Fig. 2)

Arnone and his associates found differences in the attenuation coefficients in Gulf Stream waters which reflected changes in pigment content and composition. They note that: "Pigment-dependent light absorption in surface waters has a direct influence on ocean color measurements made from satellites. Improved spectral resolution from ocean color scanners will allow detailed and synoptic absorbance measurements over large oceanic regions. An improved understanding of the relationship between pigment absorption and ocean color will permit the monitoring of biological processes on a global scale." [11]

Paerl and Millie, in their report on the workshop entitled "*Evaluation of spectrophotometric, fluorometric and high performance liquid chromatographic methods for algal pigment determinations in aquatic ecosystems*" [49] (1991) state that pigment signatures have the potential to provide valuable information on the aquatic environment. Their summary is: "...field surveys (ground truthing) coupled to aircraft or satellite-based remote sensing have the potential for enhancing our ability to detect, discriminate and quantify diagnostic chlorophyll, carotenoid, and phycobilin pigments. A key ingredient for quantitative and qualitative interpretation of remotely-sensed pigments is accurate ground truthing capable of intercalibration with remote-sensed imagery. Within the broad "chlorophyll" band available for AVHRR remote sensing (520-680 nm), Chls *a*, *b*, and *c* and respective degradation products will be detected." [49]

We quote further, from the same report, since its substance is completely pertinent to the subject addressed here: "Remote sensing is a potentially powerful tool for monitoring aquatic ecosystem dynamics on a regional scale. The feasibility of this application is due to the effect of algal pigments on water color. Current research on state-of-the-art HPLC pigment analysis, in particular accessory pigments, is important due to the taxonomic significance of specific pigments and pigment groups. An operating premise driving this research is that detection and quantitative analysis of pigments can yield information on algal population composition. This same premise applies to remote sensing, with the pigment signal determined by the optical (reflective) properties of the pigments." [49]

"Efforts are currently underway to quantify the relationship between algal spectral reflectance signatures, pigment absorbance spectra, and HPLC analyses of pigment content. The long-term goal of this work is to intersect such data quantitatively with high spectral resolution remote sensing digital data from sensors such as the 10 band AOCI (Airborne Ocean Color Imager), 220 band AVIRIS (Airborne Visible Infrared Imaging Spectrometer), and future ocean color satellite sensors such as SeaWiFS, HIRIS and MODIS-T." [49]

"Current research has focused on supervised and unsupervised classifications of Thematic Mapper data. In a highly eutrophic lake, chlorophyll maps have been constructed. These show the distribution of surface populations of cyanobacteria. Hypersaline environments in Mexico reveal population distributions of different algal and photosynthetic bacteria groups which include cyanobacteria, diatoms, halobacteria, and a high carotenoid-containing chlorophyte (*Dunaliella* sp.) This approach has successfully revealed seasonal changes of algal population distributions as well as distribution of different populations within ponds (Richardson, personal communication)." [49]

"Remote sensing of algal pigments as taxonomic indicators of algae and photosynthetic bacteria can also yield information on large-scale biogeochemical processes. In one case remote sensing is being used to scale-up field research on the taxonomically significant production of dimethyl sulfide by marine phytoplankton and its ultimate effect on cloud albedo. It has also received widespread use in estuarine ecosystems (Chesapeake Bay, San Francisco Bay, Albemarle-Pamlico Sound) as a means of evaluating synoptic-scale primary production, standing stocks of microalgae and submersed aquatic vegetation." [49]

Paerl and Millie continue with their optimistic assessment of the ability of remote sensing to contribute in an essential and particularly valuable way to aquatic ecosystem analysis. They give some suggestions as to how the combination of HPLC and remote sensing might contribute to understanding of large-scale processes: "This approach (HPLC) greatly enhances the investigator's ability to assess environmental impacts on primary production and species composition on a large scale, such as an estuary, and large segments of coastal and pelagic waters. This approach is well-suited for examining and evaluating nutrient discharges and inputs and their productive/trophic impacts over large distances. A particularly well-suited application is the assessment of frontal passages (wetfall/dryfall) as they affect primary production along trophic gradients from the upper estuary to the open ocean. Coupled to satellite/aircraft-based remote sensing, a powerful technological combination is emerging which will be capable of functionally relating physical-chemical forcing to primary production potentials, trophic state and water quality in large geographic locales." [49]

"The combined thrust of HPLC-pigment analyses and remote sensing will prove valuable in a variety of large aquaculture ecosystems. One example is the Baltic Sea where

it is suspected that enhanced nutrient loading (in large part attributable to atmospheric showers) has been linked to accelerating eutrophication in the form of nuisance cyanobacterial and chrysophyte blooms. Because these taxa can readily be discriminated by HPLC-PDAS (PDAS are photodiode array spectrophotometers) based on their unique pigment signatures, this technique may be useful in spatially and temporally distinguishing individual blooms in response to specific physical-chemical forcing events such as high precipitation, runoff, altered circulation patterns, upwelling, etc.)" [49]

"Remote sensing has additional applications in assessing pigment content and production potentials in aquaculture operations, salt evaporation ponds, sewage and effluent treatment lagoons, intertidal and subtidal reef, microbial mat and shelf benthic communities. Regional and global assessments of CO<sub>2</sub> fixation attributable to phytoplankton and benthic primary production can also be assessed remotely, by using (appropriate) algorithms. Lastly, the spatial and functional linkages between primary production and fisheries production will be far better explored using HPLC-PDAS coupled to remote sensing. Physiological condition of bloom extents from initiation to senescence and death could potentially be determined by HPLC-PDAS coupled to remote sensing, since phaeopigments and degradation products can be effectively separated and quantified." [49]

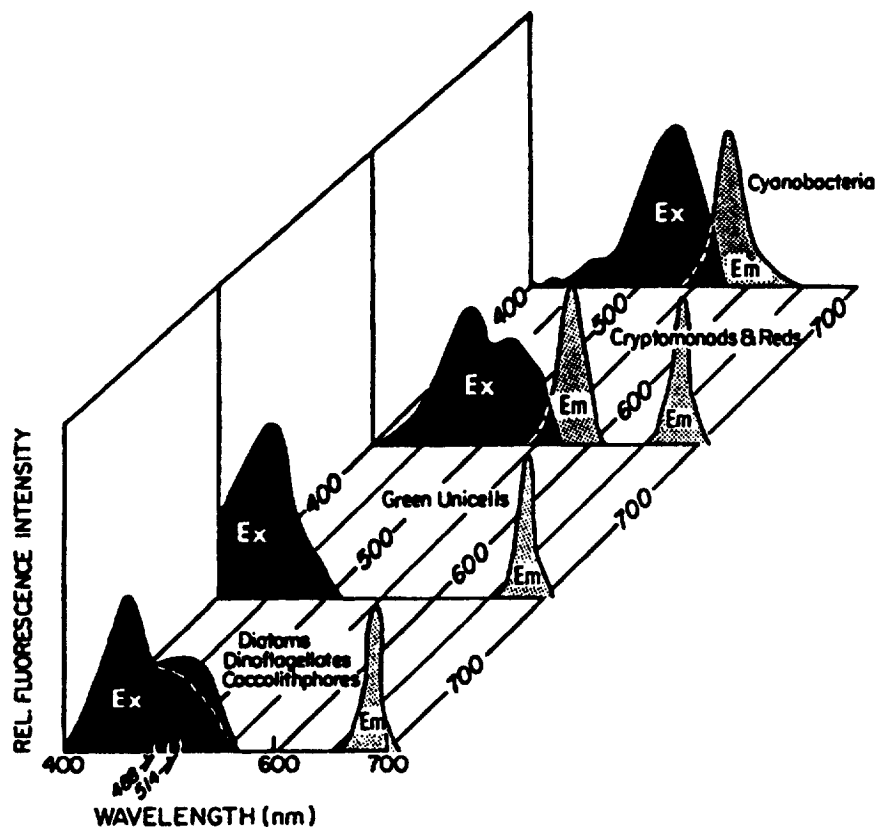
## 7. CAN PHYTOPLANKTON BE IDENTIFIED REMOTELY BY FLUORESCENCE?

Several of the algal pigments fluoresce, that is, they emit some portion of absorbed radiation. The energy of a photon absorbed by any photosynthetic pigment has three possible fates; it can dislodge an electron in a reaction which will eventually reduce carbon dioxide, i.e. carry out photosynthesis; it can be degraded as heat, or can be re-emitted as a less energetic photon, i.e. fluorescence. The chlorophylls fluoresce in the red, with a wavelength distribution peak at about 685 nm. "Dead" chlorophyll or phaeophytin also fluoresces as a consequence of the fact that the absorbed light cannot perform any chemistry. [74, 75] The phycobilins fluoresce in the green, at 560-570 nm.

A standard method of analysis for chlorophylls and phaeopigments in natural waters utilizes their red fluorescence. Fluorescence spectroscopy is about 500 times as sensitive as absorption spectroscopy in the detection of chlorophyllous pigments in methanol or acetone extract. [76] *In vivo* fluorescence is extremely useful in detecting photosynthetic organisms in water [77, 78], but the amount of fluorescence per unit chlorophyll varies with the size (and species) of organism. [74, 79, 80] Thus there is considerable scatter in any plot which relates total extracted chlorophyll with fluorescence emission in natural waters. Yentsch reviews fluorescence-pigment relationships in a very useful chapter summarizing the pertinent literature. [81]

Figure 4 summarizes the spectral fluorescence signatures of major ocean phytoplankton color groups. Note the prominent chlorophyll emission band in the red for all groups except the cyanobacteria, while the groups containing phycobilins fluoresce prominently in the green. Fluorescence in living photosynthetic organisms arises mainly from photosystem 2 rather than from photosystem 1. [80] These photosystems consist of antenna chlorophyll coupled to reaction centers. Photosystems 1 and 2 coupled together in the living organism carry out the complex series of reactions which result in the generation of a strong reductant and of oxygen as a waste molecule. The fluorescence yield of chlorophyll *a* is low in the cyanobacteria because most of the antenna chlorophyll is found in photosystem 1 which is not fluorescent (Fig. 4). [82]

However, the point to address here is whether chlorophyll fluorescence at 685 nm can be used for remote detection of phytoplankton. Platt and Sathyendranath assert that it can. We quote: "The fluorescence emission peak is at 685 nm, a wavelength for which seawater is strongly absorbing. However, solar-stimulated fluorescence by phytoplankton can be detected from ships down to at least 80 m. Furthermore, with the Fluorescence Line Imager (FLI), a high-resolution



**Figure 4. Spectral fluorescence signatures of major ocean phytoplankton color groups. (from Prezelin and Boczar, 1986 [48], modified from Yentsch and Yentsch, 1979) [94]**

sensor developed specifically to monitor this emission, high-altitude aircraft can be used to map the distribution of ocean chlorophyll. The signal-to-noise ratio of the conventional imager is just sufficient for monitoring ocean fluorescence from the top of the atmosphere, that is, from satellites, in chlorophyll-rich waters." [37]

Topliss and Platt review fluorescence theory behind the notion of monitoring the fate of photons (rather than of atoms) in order to determine productivity. They note that "It is neither a simple nor an automatic extension of these studies to consider the surface layer as viewed by remote sensing devices. The blue-green penetration for CZCS type sensors and the red fluorescence penetration for FLI sensors operate over different physical depths. Within the surface layer and deeper, many examples of photo-inhibition have been observed in active fluorescence studies, both in cloudy and sunny weather." Further, they caution that

"More understanding and study of biological mechanisms within the surface layer is called for before large scale satellite monitoring programs can be exploited to the full." [83]

The chlorophyll fluorescence signal is emitted at the same wavelengths regardless of what organism it occurs in, and thus contains no information on other pigments present. It does appear to be a promising alternative to the CZCS-type detection which depends on the ratio of blue to green backscattered light. Gower and Borstad suggested this potential more than 10 years ago. They note: "Quantitative accuracy is limited by the varying fluorescence efficiency of different phytoplankton populations and by changes in water absorption that reduce the light available for fluorescence, but this accuracy appears adequate for many survey applications." [84] Moreover, Chamberlin and his associates measured natural fluorescence in several marine environments between 2 m and 150 m depth; they assert that photosynthesis is highly correlated ( $r > 0.9$ ) with natural fluorescence. They suggest that natural fluorescence measurements, either as supplemental or direct measurements can provide a new and rapid means of estimating gross photosynthesis in the sea, as do Davis and Booth. [82, 85, 86] However, Falkowski warns that more work must be done before fluorescence measurements *per se* can replace current  $^{14}\text{C}$  or oxygen methods for measuring primary productivity. [74] He has made a start at this task and reports that variance in quantum yields and absorption cross sections decreases with increased brightness, and increases with nutrient-deficient cells. [75]

The characteristic emission wavelengths of phycobilins can be used to detect extremely small prokaryotic cells, and to determine which are cyanobacteria and which are chlorophytes. Mazel has carried out microspectrofluorometric measurements on a variety of marine organisms, and reports that phycoerythrin fluoresces at 570-580 nm and phycocyanin at 650-660 nm. [87] Olson *et al.* note that the amount of phycourobilin fluorescence per cell varies as much as 100-fold with depth [88], while Perry and Porter, using flow cytometric fluorescence, classified phytoplankton into three broad groups: cyanobacteria, prochlorophytes (which are also prokaryotic) and eukaryotes. [89]

The fluorescence of photochemical pigments thus presents an opportunity for detection of phytoplankton either due to natural (sunlight induced) fluorescence [11, 90], or excited by an artificial source of light. Maske has analyzed the modifications in the upwelling radiance signal due to the absorption of chlorophyll and its derivatives and of natural fluorescence. [91] Mitchell and Kiefer report a series of investigations on pigment-specific excitation and absorption spectra in the ocean [1], and Peacock has analyzed the contributions of fluorescence on models of remote sensing reflectance. [92] Stegman has analyzed the possibilities for using natural fluorescence to map phytoplankton pigment concentrations, and found consistently low values for the fluorescence yield. [93]

Fluorescence also has the potential of conveying information on "environmentally induced physiological changes in algae and to assess the impact individual phytoplankton species have on remotely sensed measures of ocean color. For instance, changes in the absorption and fluorescence excitation spectra of phytoplankton collected from the top and bottom of the euphotic zone, and from samples exposed to manipulated light environments have been used to determine the photoadaptive states of natural populations." [48]

While the wavelength of fluorescence emission of chlorophylls has little information about the identity of the source (i.e. which species contains that chlorophyll) the excitation spectra can potentially provide a much richer store of clues. The excitation spectrum refers to the relative efficiency of various wavelengths in the production of fluorescence from

chlorophyll. This is because the excitation energy is absorbed by the photosynthetically active accessory pigments and transferred to chlorophyll *a*. It is these carotenoid accessory pigments which are so varied among the different groups of microalgae. [94] Representative excitation spectra are illustrated in Figure 4. While considerable work has been done in characterizing the different excitation spectra, these have been in laboratory cultures. At present, there is a large gap between this type of information and applications to remote sensing.

An important advance has been reported by Hoge and Swift, who used a two-color airborne lidar system in the systematic study of several ocean features. They demonstrated a high coherence between the two-color chlorophyll *a* data and between the Nd:YAG laser-excited responses of chlorophyll *a* and phycoerythrin, concluding that this technique was a practical one for delineating water masses characterized by different planktonic assemblages. [9] Venable *et al.* modeled simulated fluorosensor signals returned from subsurface distributions of chlorophyll. [95]

## 8. GELBSTOFF, OR YELLOW MATTER

Dissolved organic matter, largely humic and fulvic acids of terrigenous origin (also used is the German term, "Gelbstoff" or yellow matter) gives water a yellow hue when in high concentrations. Gelbstoff has high absorption in the ultraviolet with an exponential decrease toward the longer wavelengths [35]. Yentsch notes that Gelbstoff is generally associated with fresh water inflow, and hence is concentrated in the upper few meters of coastal waters. [81] Both Yentsch and Kirk find that photosynthetically active radiation (PAR) is decreased in the blue part of the spectrum due to the presence of Gelbstoff. [81, 96]

What influence does Gelbstoff have on our ability to detect and characterize phytoplankton?

Carder and his associates have investigated the role of Gelbstoff in their studies of the Puget Sound area as well as the eastern Gulf of Mexico, and found that it plays a significant role in the specific absorption spectra for stations with low chlorophyll values, and can dominate the backscattering coefficient at the shorter wavelengths used in remote sensing reflectance ratios. However, they developed a site-specific chlorophyll algorithm which made possible the derivation of useful chlorophyll data; the model can also be modified to simulate the spectral reflectance of other pigment groups. [25, 35, 97] These studies again emphasize the importance of modifying algorithms as necessary for specific regions in order to derive meaningful pigment values remotely. However, Gordon and his associates have developed a semianalytic radiance model which predicts the upwelled spectral radiance at the sea surface as a function of the phytoplankton pigment concentration for waters in which the optical properties are controlled by phytoplankton and their immediate detritus (Morel Case 1 waters). This model can be extended to include Gelbstoff, and thus is useful for the identification and interpretation of deviations from Case 1 waters. [98]

Both Carder [99] and Bukata [100] and their associates developed approaches more appropriate for Morel Case 2 waters in general (i.e. containing Gelbstoff and suspended mineral particles as well). They either measure or estimate the inherent optical properties of various components of the water masses: water, chlorophyll, Gelbstoff, inorganic mineral particulates, and so forth. Given sufficient and appropriate spectral bands, the inherent

optical properties can be used to develop bio-optical algorithms for estimating the various components.

## 9. CAN ANY DISTINCTION BE MADE AT PRESENT (WITH CZCS IMAGES) AMONG DIFFERENT TYPES OF PHYTOPLANKTON?

The answer here is "yes" for several specific cases.

### 9.1 Coccolithophorids

Holligan and others [101, 102] postulated in 1983 that areas which appeared bright in CZCS images were due to the presence of the prymnesiophytes known as coccolithophorids (*Emiliana huxleyi*) and their detached plates, which are almost pure calcium carbonate. This surmise was verified when a ship was able to obtain samples from these areas. Since then, characteristic "glitter" has been observed in the north Pacific and other areas. Pigments associated with the coccolithophorids are chlorophyll *c* and fucoxanthin. [103]

A remotely detected bloom was reported by Ackleson in 1990. "In June, 1989, a coccolithophore bloom (species *Emiliana huxleyi*) formed within the southwestern portion of the Gulf of Maine. Bloom development was monitored with AVHRR visible band imagery. During the height of the bloom, a hydrographic survey was conducted to measure optical, physical, and biological properties of the euphotic layer within and adjacent to the bloom. Microscopic examination of water samples indicated that particulate material within the bloom was comprised almost entirely of *E. huxleyi* cells and detached coccoliths." [104]

The semianalytic radiance model of ocean color developed by Gordon and his associates can be modified to include the detached coccoliths, as well as the yellow substances mentioned above. Potential applications of this model include an improved bio-optical algorithm for the retrieval of pigment concentrations from satellite imagery in the presence of these coccoliths. [98]

The coccolithophorids are of particular importance to those interested in both the global carbon budget and in dimethyl sulfide (DMS). The possibility that enormous blooms of coccolithophorids may "pump" significant amounts of carbon dioxide to the bottom of the ocean to be sequestered as limestone is of importance. There is also evidence that coccolithophorids may be a source of DMS, and that this molecule is oxidized to sulfur dioxide in the atmosphere, eventually serving as cloud condensation nuclei. Again, the importance of these possible effects is of importance to models of the global climate. [105]

### 9.2 Trichodesmium (Oscillatoria)

Atmospheric nitrogen,  $N_2$ , can only be converted to a form usable by plants and algae by bacteria. Among photosynthetic bacteria, some cyanobacteria have this capability, which can be of substantial ecological importance in both freshwater and saline habitats. *Trichodesmium* is a filamentous cyanobacterium which forms large floating mats in the oceans, and which is distinguishable by a characteristic appearance in CZCS images. [55] It is probably the dominant marine diazotrophic organism, and is important to both carbon and nitrogen budgets of the upper ocean. [56] Marlon Lewis and his associates have determined the photosynthetic action, absorption and quantum yield spectra for a natural population of *Oscillatoria* in the North Atlantic. The most prominent feature of the *in vivo* absorption

spectrum is a peak at 493 nm, characteristic of a phycourobilin chromophore of phycoerythrin. [56] They raise the question of whether the presence at the sea surface of high concentrations of organisms that possess phycobiliproteins could bias the remote detection of sea-surface chlorophyll from water-leaving radiances, but conclude that little error is introduced even when *Oscillatoria* is present. [56]

### 9.3 Red and brown tides

Red or brown "tides" are dense assemblages of dinoflagellates which can have serious or even disastrous consequences. They can be toxic to fish and shellfish, creating dangerous public health problems. It is important to identify and track them. Their color is caused by characteristic carotenoids, and can be detected in CZCS images. [67, 102] Millie and Kirkpatrick note that *Gymnodinium breve* can reach concentrations of  $20 \times 10^6$  cells per liter. Since dinoflagellates have chlorophylls *a*, *c2* and *c3*, as well as fucoxanthin (but not peridinin) more precise characterization should be possible with future remote sensors. [6] Holligan *et al.* showed how the CZCS provided new information on the dynamics of dinoflagellate blooms, particularly one which had chlorophyll concentrations  $>30 \text{ mg/m}^3$  in the English Channel. [102]

Paerl and his associates have been studying the effects of nutrient loading in coastal, estuarine, and inland waters. One of the effects in coastal waters has been a disastrous red tide, which devastated shellfish and finfish industries, recreational fishing, and tourism. [106] The desirability of being able to sense these remotely is obvious. Yentsch suggests that the brown tide organism, *Aureococcus*, may have unique absorption characteristics which may make remote sensing of a bloom possible. Another possibility is to use fluorescence excitation spectra (e.g. the ratio of 530nm/430nm) for giving an indication of the type of organisms present. [107]

Sakshaug *et al.* have found a clear separation between toxic prymnesiophytes and dinoflagellates on one hand and non-toxic diatoms on the other, when ratios of blue to red, and blue to green, were compared in a beam attenuation meter. [47] They note that: "The ideal investigation in the context of in-depth studies of phytoplankton ecology is ...one which includes both remote sensing and the deployment of ships, with additional support from laboratory measurements."

## 10. SENSORS CURRENTLY SCHEDULED AND PLANNED FOR LAUNCH

Satellite oceanography began in 1972 with the first of the Landsat series of satellite instruments and the Multispectral Scanner System (MSS) which had four broad spectral bands (500-600, 600-700, 700-800, and 800-1100 nm) with a spatial resolution of 80 m covering a 100 nautical mile square area. The Thematic Mapper (TM) succeeded the MSS in 1982 with 30 m spatial resolution and a set of bands fine-tuned for terrestrial objects, primarily vegetation (450-520, 520-600, 630-690, 760-900, 1550-1750, and 2080-2360 nm as well as a thermal band). With low radiometric sensitivity and 16-18 day repeat cycles neither of these instruments was well suited for studying aquatic environments. In 1986 the French launched their Systeme Probatoire d'Observation de la Terre (SPOT) with three multispectral bands (500-590, 610-680, and 790-890 nm) at 20 m resolution with a 60 km swath. SPOT's ability to point from side-to-side improved its revisit time, but it was still a terrestrially oriented instrument.



The CZCS was the first satellite instrument to target aquatic environments specifically. Four narrow spectral bands in the visible region at 443, 520, 550, and 670 nm each 20 nm wide were selected to cover pigment absorption (443 and 670 nm) as well as the green reflectance peak (550 nm) and a "hinge point" (520 nm) noted in early spectral investigations of oceanic waters. [108] A band at 700-800 nm was designed to separate land and clouds from open water. The CZCS featured higher radiometric sensitivity (SNR ~200) than the Landsat instruments, spatial resolution of ~1 km, a swath width of 1600 km (for overlapping coverage day-to-day), and the ability to reduce sunglint by pointing away from the sun. As noted earlier, the CZCS was spectacularly successful in mapping the distribution of phytoplankton globally and as a function of time.

The CZCS approach has been expanded in the future Sea-viewing Wide Field of View Sensor (SeaWiFS) instrument scheduled to be launched in 1994 by the addition of visible bands at 412 nm (for determining Gelbstoff absorption and at 490 nm (to provide better sensitivity for measuring moderate chlorophyll concentrations) as well as two near-infrared bands at 765 and 865 nm (to aid atmospheric correction). Radiometric sensitivity was to be significantly improved (SNR ~600). [24] [109]

We quote here the goals of SeaWiFS as stated by Hooker *et al.*: "SeaWiFS ...will bring to the ocean community a welcomed and improved renewal of the ocean color remote sensing capability lost when the Nimbus-7 Coastal Zone Color Scanner (CZCS) ceased operating in 1986. The goal of SeaWiFS...is to examine oceanic factors that affect global change. Because of the role of phytoplankton in the global carbon cycle, data obtained from SeaWiFS will be used to assess the ocean's role in the global carbon cycle as well as other biogeochemical cycles. SeaWiFS data will be used to help elucidate the magnitude and variability of the annual cycle of primary production by marine phytoplankton and to determine the distribution and timing of spring blooms. The observations will help to visualize the dynamics of ocean and coastal currents, the physics of mixing, and the relationships between ocean physics and large-scale patterns of productivity." [109]

The vision of SeaWiFS's role is further elucidated by McLain and his associates: "SeaWiFS will provide routine global coverage every two days and is designed to provide estimates of photosynthetic pigment concentrations of sufficient accuracy for use in quantitative studies of the ocean's primary productivity and biogeochemistry." [110] Mueller and Austin have detailed the necessary measurement protocols. [111]

In anticipation of the improved instrument, NASA obtained an aircraft scanner, the Airborne Ocean Color Imager, that closely simulated the spectral properties and radiometric sensitivity of SeaWiFS; it lacks a 412 nm band, but it has additional bands at 620 nm and 1012 nm as well as a thermal band. [112] The 620 nm band was originally included on SeaWiFS for determining particulates in a region of minimal pigment absorption, but it was deleted in favor of the 412 nm band for determining Gelbstoff. There is a strong phycobilin absorption peak at 620 nm so this band might be useful for detecting phycobilins. The 1012 nm band was added for atmospheric correction of turbid waters. From 20 km altitude the instrument has a spatial resolution of 50 m and a swath width of 35 km. Table 3 lists the spectral and radiometric characteristics of CZCS, the Airborne Ocean Color Imager, and SeaWiFS.

**TABLE 3.** Spectral and radiometric characteristics of the Coastal Zone Color Scanner, Airborne Ocean Color Imager and SeaWiFS. Band centers and band widths (at full width, half maximum) are given in nanometers and the signal to noise ratios (SNR) use radiances expected at the top of the atmosphere. Similar bands have been aligned horizontally.

Coastal Zone Color Scanner				Airborne Ocean Color Imager				SeaWiFS			
Band No.	Band Center, nm	Band Width, nm	SNR	Band No.	Band Center, nm	Band Width nm	SNR	Band No.	Band Center, nm	Band Width nm	SNR
1	443	20	158	1	444	23	450	1	412	20	500
2	520	20	200	2	490	20	1010	2	443	20	675
3	550	20	280	3	520	21	915	3	490	20	665
4	670	20	176	4	565	20	615	4	510	20	615
5	750	100	118	5	619	21	440	5	555	20	580
				6	665	21	350	6	670	20	445
				7	772	60	360	7	765	40	455
				8	862	60	250	8	865	40	465
				9	1012	60	120				
6	11500	2000	-	10	10395	3900	-				

Beyond SeaWiFS several satellite instruments are in the planning stage. The Japanese space agency is considering plans for an instrument very similar to SeaWiFS for launch about 1995; it is being called the Ocean Color and Temperature Sensor (OCTS) and will have spectral bands with sensitivity and spatial resolution similar to SeaWiFS. One instrument originally planned to be a facility instrument for the US's Earth Observing System, the Moderate Resolution Imaging Spectrometer-Tilt (MODIS-T) was sidelined in favor of SeaWiFS during a major restructuring of the Earth Observing System. (The tilt feature is similar to the sunglint avoidance mechanism on CZCS.) Its future status is unclear, but MODIS-T was envisioned as a step beyond SeaWiFS: an imaging spectrometer with 64 contiguous spectral bands covering the 400-1040 nm spectral region with high radiometric sensitivity. Of the 64 bands, any 16 could be selected for transmission. In addition to a set of SeaWiFS bands, special applications could be accommodated. For instance, three or more bands could define the 685 nm fluorescence peak and/or an absorption feature at 620 nm. The European Space Agency is planning an instrument similar to MODIS-T for launch on the first European Earth Observing System platform to be called the Medium Resolution Imaging Spectrometer (MERIS); it will have a slightly better spatial resolution of 0.5 km instead of 1 km for all the other satellite ocean color instruments. It will cover the same spectral region and have the capability to select and transmit 15 of its 64 bands.

The Moderate Resolution Imaging Spectrometer-Nadir (MODIS-N) is still a facility instrument on Earth Observing System, but it is expected to have a significant amount of sunglint contamination because it has no sunglint avoidance mechanism. Most of MODIS-N's spectral bands mimic terrestrial bands but a few mimic those of SeaWiFS. Despite its name, MODIS-N is not an imaging spectrometer but rather a hodge-podge of spectral bands

of widely varying bandwidths and purposes. The High Resolution Imaging Spectrometer (HIRIS) is another Earth Observing System facility instrument with an unclear future status. HIRIS would have 224 contiguous spectral bands covering the 450-2400 nm region with a spectral resolution of 10 nm and a spatial resolution of 20 m. HIRIS was conceived for terrestrial applications and may not have sufficient sensitivity for aquatic studies; it does not have a sunglint avoidance mechanism either. As an imaging spectrometer, HIRIS could be useful for deciphering complex spectra in the absence of sunglint. Its sensitivity can be improved after data acquisition by averaging contiguous groups of pixels together since high resolution is less important for aquatic studies. [99]

In addition to the Airborne Ocean Color Imager, there are two other airborne instruments that are appropriate for aquatic pigment studies, the Compact Airborne Spectrographic Imager (CASI) and the Airborne Visible Infrared Imaging Spectrometer (AVIRIS). CASI is an improved version of the Fluorescence Line Imager (FLI) mentioned above and was designed for aquatic studies. CASI covers approximately the 400-900 nm spectral range with 288 contiguous bands. It has two operating modes, spatial and spectral. In spatial mode an image 512 pixels wide is acquired in 15 user-defined spectral bands. In spectral mode all 288 bands are obtained for 39 equally spaced columns across the field-of-view of the instrument. The basic reason for these limitations is the recording capability for the massive amount of data the instrument can deliver. (Data storage, retrieval and processing requirements for any imaging spectrometer are daunting.) CASI can obtain data over land and water targets without saturating the sensors due to its 12-bit dynamic range. [113, 114]

AVIRIS was designed by the Jet Propulsion Laboratory to detect mineral absorption features primarily in the 1200-2400 nm range but it was expanded to an imaging spectrometer covering the 450-2400 nm range. Recently, the instrument has been applied to detecting absorption features in plant canopies such as those due to proteins, lignin, and starch. Some workers have attempted to use AVIRIS for aquatic studies, but they have been plagued by periodic noise in the data. [115, 116] These problems may now be under control because an image of Lake Tahoe showed nothing but "white noise". [117] It remains to be seen if AVIRIS has sufficient sensitivity to be useful for oceanic studies but Carder *et al.* have shown encouraging results in coastal waters. [99] Acquiring and processing AVIRIS data to a computer compatible tape has been expensive: \$4,000 for a 512x614 pixel scene covering 11 km square in 1992.

## 11. SUMMARY AND RECOMMENDATIONS

Advances in the correlation of major taxonomic groups with characteristic accessory pigments have opened the possibility that these pigments, in turn, can be detected by means of their spectral signatures. Some progress has already been made in remote sensing of assemblages such as coccolithophorid blooms, mats of nitrogen-fixing cyanobacteria, or the huge concentrations of dinoflagellates known as red or brown tides.

Much more information about the composition of algal groups, as well as the total amount of chlorophyll and correlated primary productivity is potentially available by remote sensing. We would expect water bodies having higher phytoplankton concentrations to be more amenable to analysis of accessory pigments simply because their characteristic absorption should be more pronounced in comparison to absorption by water itself. Thus, such analysis might be more appropriate for coastal waters, estuaries, and lakes rather than oceanic waters.

If the implied emphasis on non-oceanic waters for the analysis of accessory pigments by remote sensing is correct, it will be necessary to develop the remote sensing techniques required for working with Case 2 waters. At present, the approaches using the inherent optical properties of the constituents of the water body appear to offer the best hope best hope for developing techniques for working with Case 2 waters [99, 100] but the whole area needs much work. [118]

The optical characteristics of the phytoplankton absorption and fluorescence spectra are also responsive to the nutritional status of phytoplankton, and thus make this accessible by remote sensing.

It is also clear that none of the satellite sensors now known to be in the preparation stage is ideal from the point of view of what we might wish to know. Each represents a number of compromises among ideals, costs, and other considerations of feasibility. We here mention some of the shortcomings of SeaWiFS, as the detector which will soon be providing data of the type that has been completely absent since the demise of CZCS in 1986. The biggest gap is between 555 nm and 670 nm. Both the absorption and fluorescence bands of the phycobilins are prominent in this interval. The recent discoveries of the enormous role played by the very small cyanobacteria in the overall carbon budget make the omission of bands at 562 nm and 615 nm which are the absorption bands of phycoerythrobilin and phycocyanin, respectively, (Figure 3) a major regret. In addition, a major component of the global nitrogen cycle is the cyanobacterial nitrogen-fixer, *Trichodesmium*. Band 3, centered at 490 nm, might prove to be useful for its detection. [56] Fortunately, this band is included in most future instruments.

The alpha bands of chlorophylls *a*, *b*, and *c*, are distinct, but their distributions arise in the red end of the spectrum where water absorbs strongly. The alpha bands are more closely grouped in the blue region of the spectrum, and moreover may always be masked by the carotenoids abundant in phytoplankton (see Figure 2). However, the feasibility of differentiating these chlorophylls should be thoroughly explored even if only for higher chlorophyll concentrations where the chlorophyll would be closer to the surface and water absorption would be less significant.

The wavelengths of fluorescence emission can clearly indicate the presence of the phycobilins characteristic of cyanobacteria (green to yellow) *versus* chlorophyll (red, 685 nm). These emission bands clearly have the potential to differentiate the prokaryotes which are extremely small but abundant, from the better-known eukaryotic algae. At minimum, detection of the 685 nm fluorescence requires three carefully selected bands around the 685 peak. The present 670 nm band might be one of them, so only two additional bands might be required, say 685 and 695 nm. Virtually no remote sensing investigations examined phycobilin fluorescence, so selection of any bands in the green to yellow region would be premature. Moreover, a number of the active researchers in the field of oceanic remote sensing are enthusiastic about the possibility of fluorescence excitation spectra as a sensitive probe for determining which pigments are photosynthetically active in absorbing radiation used for photosynthesis. For instance, 530 nm light is very effective in exciting fluorescence in dinoflagellates and diatoms, and not at all effective for green algae. [94] Yet technology applicable to determining fluorescence excitation spectra has not advanced very far, to our knowledge.

In view of the richness of spectral information potentially available, it would seem wise to pursue the development of an instrument with the planned characteristics of the imaging spectrometers MODIS-T and/or MERIS. Chlorophyll fluorescence and phycobilin absorption both require contiguous bands for proper detection. The same is likely to be true of a method for differentiating chlorophylls *a*, *b*, and *c*, in the red region.

Recent advances in the pigment analysis have been tremendous, thanks largely to the power of HPLC. The task of linking these pigments to specific groups of phytoplankton, and of using them to extract information about status of these organisms is progressing rapidly. It is to be hoped that this work will be well supported and also that its application to the design of airborne and satellite sensors will go forward without hindrance. If all potential information about the distribution and dynamics of phytoplankton can be gathered by all means (remote, *in situ*, and shipboard) and thoroughly analyzed, understanding of the global ecology of the oceans will be greatly advanced. The largest potential gains would appear to be in coastal, or Case 2, waters where some 40% of the total global primary production arises and which had to be ignored by the CZCS due to the complexity of those waters.

## 12. REFERENCES CITED

1. Mitchell, B.G. and D.A. Kiefer, *Variability in pigment specific particulate fluorescence and absorption spectra in the northeastern Pacific Ocean*. Deep-Sea Research, 1988. **35**(5): p. 665-689.
2. Millie, D.F., M.C. Baker, C.S. Tucker, B.T. Vinyard, and C. Dionigi, *High-resolution airborne remote sensing of bloom-forming phytoplankton*. J. Phycol., 1992. **28**: p. 281-290.
3. Richardson, L.L., D. Bachoon, V. Ingram-Willey, C.C. Chow, and K. Weinstock. *Remote sensing of the biological dynamics of large-scale salt evaporation ponds*. In *24th International Symposium on Remote Sensing of the Environment*. 1991. Rio de Janeiro, Brazil, 27-31 May, **2**: p. 611-623.
4. Bidigare, R.R., J.H. Morrow, and D.A. Kiefer. *Derivative analysis of spectral absorption by phytoplankton pigments*. In *Ocean Optics IX*. 1988. Orlando, FL **925**: p. 101-108. Society of Photo-Optical Instrumentation Engineers (SPIE).
5. Bidigare, R.R., J.H. Morrow, and D.A. Kiefer, *Derivative analysis of spectral absorption by photosynthetic pigments in the western Sargasso Sea*. J. Mar. Res., 1989. **47**(2): p. 323-341.
6. Millie, D.F. and G.J. Kirkpatrick. *Investigating the pigment signature of Gymnodinium breve: Are HPLC and remote-sensing technologies applicable for routine monitoring of coastal assemblages?* In *Aquatic Sciences Meeting*, Am. Soc. Limnol. Oceanogr. 1992. Santa Fe, NM.
7. Malone, T.C., P.G. Falkowski, T.S. Hopkins, G.T. Rowe, and T.E. Whitledge, *Mesoscale response of diatom populations to a wind event in the plume of the Hudson River*. Deep-Sea Res., Part A: Oceanographic Research Papers, 1983. **30**(2A): p. 149-170.

8. Prezelin, B.B., R.R. Bidigare, H.A. Matlick, M. Putt, and B. Ver Hoven, *Diurnal patterns of size-fractionated primary productivity across a coastal front*. Mar. Biol., 1987. **96**(4): p. 563-574.
9. Hoge, F.E. and R.N. Swift, *Airborne dual laser excitation and mapping of phytoplankton photopigments in a Gulf Stream Warm Core Ring*. Applied Optics, 1983. **22**: p. 2272-2280.
10. Richardson, L.L., *Optical properties of naturally occurring populations of algae and photosynthetic bacteria*. Eos, 1990. **71**(2): p. 109.
11. Arnone, R.A., R.R. Bidigare, C.C. Trees, and J.M. Brooks. *Comparison of the attenuation of spectral irradiance and phytoplankton pigments within frontal zones*. In *Ocean Optics VIII*. 1986. Orlando, FL **637**: p. 126-130. SPIE.
12. Bidigare, R.R., J. Marra, T.D. Dickey, R. Itturiaga, K.S. Baker, R.C. Smith, and H. Pak, *Evidence for phytoplankton succession and chromatic adaptation in the Sargasso Sea during spring 1985*. Mar. Ecol. (Prog. Ser.), 1990. **60**(1-2): p. 113-122.
13. Hovis, W., E.F. Szajna, and W.A. Bohan, *Nimbus-7 CZCS Coastal Zone Color Scanner Imagery for Selected Coastal Regions*. 1988, NASA Goddard Space Flight Center.
14. Morel, A. and J. Berthon, *Surface pigments, algal biomass profiles, and potential production of the euphotic layer: Relationships reinvestigated in view of remote-sensing applications*. Limnol. Oceanogr., 1989. **34**: p. 1545-1562.
15. Esaias, W.E., G.C. Feldman, C.R. McClain, and J.A. Elrod, *Monthly satellite-derived phytoplankton pigment distribution for the North Atlantic ocean basin*. Eos, 1986. **67**(44): p. 835-837.
16. Platt, T. and A.W. Herman, *Remote sensing of phytoplankton in the sea - Surface-layer chlorophyll as an estimate of water-column chlorophyll and primary production*. Int. J. of Remote Sensing, 1983. **4**(Apr-June): p. 343-351.
17. Eppley, R.W., E. Stewart, M.R. Abbott, and R.W. Owen. *Estimating ocean production from satellite-derived chlorophyll - Insights from the EASTROPAC data set*. in *Symposium on Vertical Motion in the Equatorial Upper Ocean and Its Effects Upon Living Resources*. 1985. Paris.
18. Balch, W.M., R.W. Eppley, and M.R. Abbott, *Remote sensing of primary production - II. A semi-analytical algorithm based on pigments, temperature and light*. Deep Sea Research, 1989. **36**(8): p. 1201-1217.
19. Hayward, T.L. and E.L. Venrick, *Relation between surface chlorophyll, integrated chlorophyll and integrated primary production*. Marine Biology, 1982. **69**: p. 247-252.
20. Kiefer, D.A. *Biological sources of optical variability in the sea*. In *Ocean Optics VIII*. 1986. Orlando, FL **637**: p. 25-34. SPIE.
21. Platt, T. and K. Denman, *Patchiness in phytoplankton distribution*. In *The Physiological Ecology of Phytoplankton*, I. Morris, Editor. 1980, University of California Press: Berkeley and Los Angeles. p. 413-431.

22. Mitchell, B.G., R. Iturriaga, and D. Kiefer. *Variability of particulate spectral absorption coefficients in the eastern Pacific Ocean*. In *Ocean Optics VII*. 1984. Monterey, CA 489: p. 113-118. SPIE.
23. Prezelin, B.B. and H.A. Matlick, *Primary production in marine snow during and after an upwelling event*. *Limnol. Oceanogr.*, 1983. 28(6): p. 1156-1167.
24. Balch, W.M., *Primary production by satellite - Sharpening Occam's razor*. In *Aquatic Sciences Meeting*, Am. Soc. Limnol. Oceanogr., 1992, Santa Fe, NM.
25. Carder, K.L., R.G. Steward, J.H. Paul, and G.A. Vargo, *Relationships between chlorophyll and ocean color constituents as they affect remote-sensing reflectance models*. *Limnol. Oceanogr.*, 1986. 31(2): p. 403-413.
26. Eppley, R.W., E. Stewart, M.R. Abbott, and U. Heyman, *Estimating ocean primary production of satellite chlorophyll - Introduction to regional differences and statistics for the Southern California Bight*. *J. of Plankton Res.*, 1985. 7(1): p. 57-70.
27. Mueller, J.L., C.C. Trees, and R.A. Arnone. *Evaluation of Coastal Zone Color Scanner diffuse attenuation coefficient algorithms for application to coastal waters*. In *Ocean Optics X*. 1990. Orlando, FL 1302: p. 72-78. SPIE.
28. Sathyendranath, S. and T. Platt, *Remote sensing of ocean chlorophyll - consequence of nonuniform pigment profile*. *Applied Optics*, 1989. 28(Feb. 1): p. 490-495.
29. Smith, R.C., R.R. Bidigare, B.B. Prezelin, K.S. Baker, and J.M. Brooks, *Optical characterization of primary productivity across a coastal front*. *Mar. Biol.*, 1987. 96(4): p. 575-591.
30. Smith, R.C., B.B. Prezelin, R.R. Bidigare, and K.S. Baker, *Bio-optical modeling of photosynthetic production in coastal waters*. *Limnol. Oceanogr.*, 1989. 34(8): p. 1524-1544.
31. Balch, W., R. Evans, J. Brown, G. Feldman, C. McClain, and W. Esaias, *The remote sensing of ocean primary productivity: Use of a new data compilation to test satellite algorithms*. *J. of Geophysical Res.*, 1992. 97(C2 (Feb. 15, 1992)): p. 2279-2293.
32. Banse, K. and C.R. McClain, *Winter blooms of phytoplankton in the Arabian Sea as observed by the Coastal Zone Color Scanner*. *Mar. Ecol. (Prog. Ser.)*, 1986. 34(Dec. 19): p. 201-211.
33. Mitchell, B.G. *Algorithms for determining the absorption coefficient of aquatic particulates using the quantitative filter technique (QFT)*. In *Ocean Optics X*. 1990. Orlando, FL 1302: p. 137-148. SPIE.
34. Balch, W.M., M.R. Abbott, and R.W. Eppley, *Remote sensing of primary production - I. A comparison of empirical and semi-analytical algorithms*. *Deep-Sea Research*, 1989. 36(2): p. 281-295.

35. Carder, K.L., D.J. Collins, M.J. Perry, H.L. Clark, J.M. Mesias, J.S. Cleveland, and J. Greenier. *The interaction of light with phytoplankton in the marine environment*. In *Ocean Optics VIII*. 1986. Orlando, FL 637: p. 42-55. SPIE.
36. Cleveland, J.S., W.S. Chamberlain, J.H. Morrow, R. Iturriaga, R.R. Bidigare, M.J. Perry, and D.A. Siegel, *Estimation of the phytoplanktonic component of particulate light absorption: An evaluation of approaches*. *Eos*, 1990. 71(2): p. 109.
37. Platt, T. and S. Sathyendranath, *Oceanic primary production: estimation by remote sensing at local and regional scales*. *Science*, 1988. 241: p. 1613-1620.
38. Collins, D.J., D.A. Kiefer, J.B. Soohoo, C. Stallings, and W.-L. Yang. *A model for the use of satellite remote sensing for the measurement of primary production in the ocean*. In *Ocean Optics VIII*. 1986. Orlando, FL 637: p. 335-348. SPIE.
39. Prezelin, B.B., H.E. Glover, and L. Campbell, *Effects of light intensity and nutrient availability on diel patterns of cell metabolism and growth in populations of Synechococcus spp.* *Mar. Biol.*, 1987. 95(3): p. 469-480.
40. Bidigare, R.R., D. Schofield, and B.B. Prezelin, *Influence of zeaxanthin on quantum yield of photosynthesis of Synechococcus clone WH7803 (DC2)*. *Mar. Ecol. (Prog. Ser.)*, 1989. 56(1-2): p. 177-188.
41. Reid, F.M.H., E. Stewart, R.W. Eppley, and D. Goodman, *Spatial distribution of phytoplankton species in chlorophyll maximum layers off southern California*. *Limnol. Oceanogr.*, 1978. 23(2): p. 219-226.
42. Eppley, R.W. *Relations between primary production and ocean chlorophyll determined by satellites*. in *Global Ocean Flux Study Workshop*. 1984. Woods Hole, MA.
43. Bidigare, R.R., R.C. Smith, K.S. Baker, and J. Marra, *Oceanic primary production estimates from measurements of spectral irradiance and nutrient concentrations*. *Global Biogeochemical Cycles*, 1987. 1(3): p. 171-186.
44. Arvesen, J.C., J.P. Millard, and E.C. Weaver. *Rapid assessment of water pollution by airborne measurement of chlorophyll content*. in *Joint Conference on Sensing of Environmental Pollutants*. 1971. Palo Alto, CA.
45. Arvesen, J.C., J.P. Millard, and E.C. Weaver, *Remote sensing of chlorophyll and temperature in marine and fresh waters*. *Astronautica Acta*, 1973. 18: p. 229-239.
46. Weaver, E.C. and J.C. Arvesen, *Aerial determination of chlorophyll content in marine and fresh waters*, *Eos*, 1971. 52: p. 345.
47. Sakshaug, E., G. Johnsen, O. Samseth, and Z. Volent. *Identification of phytoplankton blooms by means of remote sensing*. In *Environment Northern Seas*. 1991. p. 91-100.
48. Prezelin, B.B. and B.A. Boczar, *Molecular bases of cell absorption and fluorescence in phytoplankton: potential applications to studies in optical oceanography*. In *Progress in Phycological Research*, F. Round and D. Chapman, Editors, 1986. Elsevier Science Publishers; Biopress Ltd.: p. 350-465.



49. Paerl, H.W. and D.F. Millie. *Evaluations of spectrophotometric, fluorometric and High Performance Liquid Chromatographic methods for algal pigment determinations in aquatic ecosystems*. 1991. United States Environmental Protection Agency.
50. Li, W.K.W., D.V. Subba Rao, W.G. Harrison, J.C. Smith, J.J. Cullen, B. Irwin, and T. Platt, *Autotrophic picoplankton in the tropical ocean*. Science, 1983. **219**: p. 292-295.
51. Platt, T., D.V. Subba Rao, and B. Irwin, *Photosynthesis of picoplankton in the oligotrophic ocean*. Nature, 1983. **301**(24 Feb.): p. 702-704.
52. Glover, H.E., B.B. Prezelin, L. Campbell, and M. Wyman, *Pico- and ultra-plankton Sargasso Sea communities: Variability and comparative distributions of Synechococcus species and algae*. Mar. Ecol. (Prog. Ser.), 1988. **49**(1-2): p. 127-139.
53. Hooks, C.E., R.R. Bidigare, M.D. Keller, and R.R.L. Guillard, *Coccolid eukaryote marine ultraplankters with four different HPLC pigment signatures*. J. Phycol., 1988. **24**(4): p. 571-580.
54. Paerl, H.W., *Physiological ecology and regulation of N<sub>2</sub> fixation in natural waters*. In *Advances in Microbial Ecology*, K.C. Marshall, Editor, 1990. Plenum Publishing: p. 305-344.
55. Subramanian, A., P. Falkowski, D.G. Capone, and E.J. Carpenter. *Does Tricodesmium facilitate "echo blooms" of phytoplankton?* In *Aquatic Sciences Meeting*, Am. Soc. Limnol. Oceanogr., 1992. Santa Fe, NM.
56. Lewis, M.R., O. Ulloa, and R. Platt, *Photosynthetic action, absorption, and quantum yield spectra for a natural population of Oscillatoria in the North Atlantic*. Limnol. Oceanogr., 1988. **33**: p. 92-98.
57. Paerl, H.W., *Ecophysiological and trophic implications of light-stimulated amino acid utilization in marine picoplankton*. Applied and Environmental Microbiology, 1991. **57**(2): p. 473-479.
58. Chisholm, S.W., R.J. Olson, E.R. Zettler, R. Goericke, J.B. Waterbury, and N.A. Welschmeyer, *A novel free-living prochlorophyte abundant in the oceanic euphotic zone*. Nature, 1988. **334**: p. 340-343.
59. Jeffrey, S.W., M. Sielicke, and F.T. Haxo, *Chloroplast pigment patterns in dino-flagellates*. J. Phycol., 1975. **11**: p. 374-384.
60. Jeffrey, S.W., *Algal pigment systems*, in *Primary Productivity in the Sea*, P.G. Falkowski, Editor, Plenum Press, New York and London, 1980. p. 531.
61. Wright, S.W., S.W. Jeffrey, R.F.C. Mantoura, C.A. Llewellyn, T. Bjornland, D. Repeta, and N. Welschmeyer, *Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton*. Mar. Ecol. (Prog. Ser.), 1991. **77**: p.193-196.
62. Hurley, J.P. and C.J. Watras, *Identification of bacteriophylls in lakes via reverse-phase HPLC*. Limnol. Oceanogr., 1991. **36**(2): p. 307-315.

63. Tester, P.A. and M.A. Geesey. *Spring bloom 1991, natural phytoplankton assemblages: Can HPLC pigment analyses detect taxa changes?* In *Aquatic Sciences Meeting*, Am. Soc. Limnol, Oceanogr., 1992. Santa Fe, NM.
64. Ondrusek, M.E., R.R. Bidigare, S.T. Sweet, D.A. Defreitas, and J.M. Brooks, *Distribution of phytoplankton pigments in the North Pacific Ocean in relation to physical and optical variability*. Deep-Sea Research, 1991. **38**(2): p. 243-266.
65. Bidigare, R.R., M.C. Kennicut II, and J.M. Brooks, *Rapid determination of chlorophylls and their degradation products by high-performance liquid chromatography*. Limnol. Oceanogr., 1985. **30**(2): p. 432-435.
66. Everitt, D.A., S.W. Wright, J.K. Volkman, D.P. Thomas, and E.J. Lindstrom, *Phytoplankton community compositions in the western equatorial Pacific determined from chlorophyll and carotenoid pigment distributions*. Deep-Sea Research, 1990. **37**(6): p. 975-997.
67. Levandowsky, M., *The use of satellite-based remote sensing for monitoring the brown tide phenomenon.*, The Suffolk County Health Services Dept., 1990.
68. Bidigare, R.R., T.J. Frank, C. Zastrow, and J.M. Brooks, *The distribution of algal chlorophylls and their degradation products in the Southern Ocean*. Deep-Sea Res., 1986. **33**(7A): p. 923-937.
69. Reese, C., L.L. Richardson, F.P. Chavez, K.R. Buck, and T. Bates. *Phytoplankton population assessment by measurement of in situ spectral reflectance and accessory pigments*. In *Aquatic Sciences Meeting*, Am. Soc. Limnol. Oceanogr., 1992. Santa Fe, NM.
70. Shapiro, L.P., E.M. Haugen, M.D. Keller, R.R. Bidigare, L. Campbell, and R.R.L. Guillard, *Taxonomic affinities of marine coccoid ultraphytoplankton: A comparison of immunochemical surface antigen cross-reactions and HPLC chloroplast pigment signatures*. J. Phycol., 1989. **25**(4): p. 794-797.
71. Goodwin, T.W., *The Biochemistry of Carotenoids*. Chapman and Hall, London, 1980.
72. Nelson, N.B., B.B. Prezelin, and R.R. Bidigare, *Phytoplankton light absorption and the package effect in California coastal waters*. Mar. Ecol. (Prog. Ser.), **94**: p. 217-227.
73. Ackleson, S.G., J.J. Cullen, J. Brown, and M.P. Lesser. *Some changes in the optical properties of marine phytoplankton in response to high light intensity*. In *Ocean Optics X*. 1990. Orlando, FL **1302**: p. 238-249. SPIE.
74. Falkowski, P.G. and D.A. Kiefer, *Chlorophyll a fluorescence in phytoplankton: Relationship to photosynthesis and biomass*. J. Plankton Res., 1985. **7**(5): p. 715-731.
75. Falkowski, P.G. *Measurements of biophysical parameters used to derive phytoplankton photosynthetic rates by pump and probe fluorometry*. In *Aquatic Sciences Meeting*, Am. Soc. Limnol. Oceanogr., 1992. Santa Fe, NM.

76. Cullen, J.J., C.M. Yentsch, T.L. Cucci, and H.L. MacIntyre. *Autofluorescence and other optical properties as tools in biological oceanography*. In *Ocean Optics IX*. 1988. Orlando, FL 925: p.149-156. SPIE.
77. Marra, J., C. Langdon, W.S. Chamberlin, T. Dickey, T. Granata, and D.A. Siegel, *Productivity at the seasonal time scale: An optical view*, Eos, 1990. 71: p. 108.
78. Bartz, R., R.W. Spinrad, and J.C. Kitchen. *A low power, high resolution, in situ fluorometer for profiling and moored applications in water*. In *Ocean Optics IX*. 1988. Orlando, FL 925: p. 157-170. SPIE.
79. Alpine, A.E. and J.E. Cloern, *Differences in in vivo fluorescence yield between three phytoplankton size classes*. J. Plankton Res., 1985. 7(3): p. 381-390.
80. Mitchell, B.G. and D.A. Kiefer, *Chlorophyll a specific absorption and fluorescence excitation spectra for light-limited phytoplankton*. Deep-Sea Research, 1988. 35: p. 639-663.
81. Yentsch, C.S., *Light attenuation and phytoplankton photosynthesis*, in *The Physiological Ecology of Phytoplankton*, I. Morris, Editor. University of California Press: Berkeley and Los Angeles, 1980. p. 95-127.
82. Chamberlin, W.S., C.R. Booth, D.A. Kiefer, J.H. Morrow, and R.C. Murphy, *Evidence for a simple relationship between natural fluorescence, photosynthesis and chlorophyll in the sea*. Deep Sea Res., 1990. 36(6): p. 951-973.
83. Topliss, B.J. and T. Platt, *Passive fluorescence and photosynthesis in the ocean; implications for remote sensing*. Deep Sea Res., 1986. 33(7): p. 849-864.
84. Gower, J.F.R. and G. Borstad, *Use of the in vivo fluorescence line at 685 nm for remote sensing surveys of surface chlorophyll a*. In *Oceanography from Space*, J.F.R. Gower, Editor. 1981, Plenum, New York. p. 329-338.
85. Chamberlin, W.S., J. Marra, R.A. Reynolds, D.A. Kiefer, and C.R. Booth, *Consideration of factors which affect the relationship between photosynthesis and natural fluorescence*, Eos, 1990. 71: p. 108.
86. Davis, R.F. and C.R. Booth, *Correlation between solar-induced fluorescence and primary production*, Eos, 1987. 68: p. 1694.
87. Mazel, C. *Spectral transformation of downwelling radiation by autofluorescent organisms in the sea*. In *Ocean Optics X*. 1990. Orlando, FL 1302: p. 320-327. SPIE.
88. Olson, R.J., S.W. Chisholm, E.R. Zettler, and E.V. Armbrust, *Pigments, size, and distribution of Synechococcus in the North Atlantic and Pacific Oceans*. Limnol. Oceanogr., 1990. 35(1): p. 45-58.
89. Perry, M.J. and S.M. Porter, *Temporal changes in the relative contribution of major phytoplankton groups to absorption in the Sargasso Sea*. Eos, 1990. 71(2): p. 109.
90. Kim, H.H. and H. van der Piepen. *Sunlight induced 685 nm fluorescence imagery*. In *Ocean Optics VIII*. 1986. Orlando, FL 637: p. 358-363. SPIE.

91. Maske, H., *The effect of chlorophyll degradation products on the remote sensing signal of natural in vivo fluorescence*, Eos, 1987. **68**: p. 1694.
92. Peacock, T.G., K.L. Carder, C.O. Davis, and R.G. Steward. *Effects of fluorescence and water Raman scattering on models of remote sensing reflectance*. In *Ocean Optics X*, 1990. Orlando, FL 1302: p. 303-319. SPIE.
93. Stegman, P., *Solar-stimulated fluorescence and its implications for remote sensing*, Eos, 1987. **68**: p. 1694.
94. Yentsch, C.S. and C.M. Yentsch, *Fluorescent spectral signatures: The characterization of phytoplankton populations by the use of excitation and emission spectra*. J. Mar. Res., 1979. **37**: p. 471-483.
95. Venable, D.D., S. Khatun, L. Poole, and A. Punjabi. *Simulated laser fluorosensor from subsurface chlorophyll distributions*. In *Ocean Optics VIII*. 1986. Orlando, FL **637**: p. 364-371. SPIE.
96. Kirk, J.T.O., *Spectral distribution of photosynthetically active radiation in some south-eastern Australian waters*. Australian J. of Marine and Freshwater Res., 1979. **30**(1): p. 81-91.
97. Carder, K.L. and R.G. Steward, *A remote-sensing reflectance model of a red-tide dinoflagellate off west Florida*. Limnol. Oceanogr., 1985. **30**(2): p. 286-298.
98. Gordon, H.R., O.B. Brown, R.H. Evans, J.W. Brown, R.C. Smith, K.S. Baker, and D.K. Clark, *A semianalytic radiance model of ocean color*. J. of Geophys. Res., 1988. **93**(D9): p. 10909-10924.
99. Carder, K.L., R.G. Steward, R.F. Chen, S. Hawes, Z. Lee, and C.O. Davis, *AVIRIS calibration and application in coastal oceanic environments: tracers of soluble and particulate constituents of the Tampa Bay coastal plume*. Photogramm. Eng. Rem. Sens., 1993. **59**(3): p. 339-344.
100. Bukata, R.P., J.H. Jerome, K.Y. Kondratyev, and D.V. Podznyakov, *Estimation of organic and inorganic matter in inland waters: optical cross sections of Lakes Ontario and Ladoga*. J. Great Lakes Res., 1991. **17**(4): p. 461-469.
101. Holligan, P.M., M. Voillier, D.S. Harbour, P. Camus, and M. Champagne-Phillippe, *Satellite and ship studies of coccolithophore production along a continental shelf edge*. Nature, 1983. **304**(28 July): p. 339-342.
102. Holligan, P.M., M. Voillier, C. Dupouy, and J. Aiken, *Satellite studies on the distribution of chlorophyll and dinoflagellate blooms in the western English Channel*. Continental Shelf Res., 1983. **2**: p. 81-96.
103. Hallegraeff, G.M., *Seasonal study of phytoplankton pigments and species at a coastal station off Sydney: Importance of diatoms and the nanoplankton*. Mar. Biol., 1981. **61**: p. 107-118.

104. Ackleson, G., *What happened during the 1989 Gulf of Maine coccolithophore bloom?* 1990. *Eos*, **71**: p. 108.
105. Schofield, O., R.R. Bidigare, and B. Prezelin, *Spectral photosynthesis, quantum yield and blue-green light enhancement of productivity rates in the diatom *Chaetoceros gracile* and the prymnesiophyte *Emiliana huxleyi**. *Mar. Ecol. (Prog. Ser.)*, 1990. **64**: p. 175-186.
106. Paerl, H.W., J. Rudek, and M.A. Mallin, *Stimulation of phytoplankton production in coastal waters by natural rainfall inputs: nutritional and trophic implications*. *Marine Biology*, 1990. **107**: p. 247-254.
107. Yentsch, C., D.A. Phinney, and L. Shapiro. *Absorption and fluorescent characteristics of the brown tide chrysophyte: its role in light reduction in coastal marine environments*. In *Novel Phytoplankton Blooms: Causes and Impact of Recurrent Brown Tides and Other Unusual Blooms*. 1988. SUNY, Stonybrook, NY: Springer-Verlag.
108. Austin, R.W. and T.J. Petzold, *The determination of the diffuse attenuation coefficient of sea water using the Coastal Zone Color Scanner*. In *Oceanography from Space*, J.F.R. Gower, Editor. 1981, Plenum Publishing Corporation: p. 239-256.
109. Hooker, S.B., W.E. Esaias, G.C. Feldman, W.W. Gregg, and C.R. McClain, *An overview of SeaWiFS and ocean color*. NASA Technical Memorandum 104566, Vol. 1, 1992. NASA, Goddard Space Flight Center, Greenbelt, MD 20771.
110. McClain, C.R., W.E. Esaias, W. Barnes, B. Guenther, D. Endres, S.B. Hooker, B.G. Mitchell, and R. Barnes, *SeaWiFS calibration and validation plan*, NASA Technical Memorandum 104566, Vol. 3, 1992. NASA, Goddard Space Flight Center, Greenbelt, MD 20771.
111. Mueller, J.L. and R.W. Austin, *Ocean optics protocols for SeaWiFS validation*. NASA Technical Memorandum 104566, Vol. 5, 1992. NASA, Goddard Space Flight Center, Greenbelt, MD 20771.
112. Wrigley, R.C., S.A. Klooster, R.S. Freedman, M. Carle, R.E. Slye, and L.F. McGregor, *The Airborne Ocean Color Imager: System description and image processing*. *J. of Imaging Technology*, 1992. **36**(5): p. 423-430.
113. Borstad, G.A. and D.A. Hill. *Using visible range imaging spectrometers to map ocean phenomena*. In *Proc. Advanced Optical Instrumentation for Remote Sensing of the Earth's Surface from Space*, 1989. Paris, France 1129: p. 130-136. SPIE.
114. Borstad, G.E., D.A. Hill, and R.C. Kerr. *Use of the Compact Airborne Spectrographic Imager (CASI): laboratory examples*. In *12th Canadian Symposium on Remote Sensing*, 1989. IGARSS. Digest: p. 2081-2084.
115. Melack, J.M. and S.H. Pilorz. *Reflectance spectra from eutrophic Mono Lake, California, measured with the Airborne Visible and Infrared Imaging Spectrometer (AVIRIS)*. In *Second Airborne Visible/Infrared Imaging Spectrometer Workshop*, 1990. Jet Propulsion Laboratory, p. 232-242.

116. Pilorz, S.H. and C.O. Davis. *Investigations of ocean reflectance with AVIRIS data*. In *Second Airborne Visible/Infrared Imaging Spectrometer Workshop*, 1990. Jet Propulsion Laboratory, p. 224-231.
117. Hamilton, M.K., C.O. Davis, S.H. Pilorz, W.J. Rhea, and K.L. Carder. *Examination of chlorophyll distribution in Lake Tahoe, using the Airborne Visible/Infrared Imaging Spectrometer (AVIRIS)*. In *Third Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) Workshop*, 1991. Jet Propulsion Laboratory, p. 289-301.
118. Bukata, R.P., J.H. Jerome, K.Y. Kondratyev, and D.V. Pozdnyakov, *Satellite monitoring of optically-active components of inland waters: an essential input to regional climate change impact studies*. *J. Great Lakes Res.*, 1991. 17(4): p. 470-478.

### 13. APPENDIX

An annotated bibliography of references concerned with the effect of phytoplankton groups on water color, with special reference to remote sensing.

1. Abayachi, J.K. and J.P. Riley, *The determination of phytoplankton pigments by high-performance liquid chromatography*. Analytica Chimica Acta, 1979. 107: p. 1-11.

A simple high-performance liquid chromatographic method is described for the determination of chlorophylls, chlorophyll degradation products, and carotenoids in phytoplankton cultures and marine particulate matter. Pigment extraction is carried out with acetone and methanol. After evaporation of the combined extracts under reduced pressure, the pigments are separated on a Particil-10 stationary phase with a mobile phase consisting of light petroleum, acetone, dimethyl sulphoxide and diethylamine. When chlorophyll *c* is present, a further development is performed with a similar, but more polar, solvent mixture. Detection is carried out spectrophotometrically at 440 nm. The method has a sensitivity for the chlorophylls of *ca.* 80 ng, and for carotene of *ca.* 5 ng. The coefficient of variation of the chromatographic stage of the procedure lies in the range 0.6-1.8%.

Dept. of Oceanography, University of Liverpool, P.O. Box 147, Liverpool L69 3BX  
(Gt. Britain)

2. Abbott, M.R. and P.M. Zion, *Satellite observations of phytoplankton variability during an upwelling event*. Continental Shelf Research, 1985. 4: p. 661-680.

A sequence of satellite images of near-surface phytoplankton pigment concentrations and sea surface temperature together with concurrent surface measurements is used to study an upwelling event during the Coastal Ocean Dynamics Experiment (CODE) off northern California. These data sets show a high degree of temporal and spatial variability during this episode. Recurrent patterns in this variability give insight into the dynamics of coastal upwelling and its effects on biological distributions. Simple models of coastal upwelling cannot explain the observed phenomena in the CODE region. Satellite estimates of phytoplankton growth rates were about  $0.9 \text{ day}^{-1}$  near persistent upwelling centers. Scripps Institution of Oceanography A-002, La Jolla, CA 92093 and Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA 91109

3. Abbott, M.R. and P.M. Zion, *Spatial and temporal variability of phytoplankton pigment off Northern California during Coastal Ocean Dynamics Experiment 1*. J. Geophys. Res., 1987. 92(C2): p. 1745-1755.

The distribution of phytoplankton pigment during the 1981 Coastal Ocean Dynamics Experiment (CODE) was examined using Coastal Zone Color Scanner (CZCS) imagery. Twenty-five CZCS images were of sufficient quality to be used for further analysis. The distribution of the data was dependent on the patterns of wind forcing, with the data set biased toward regions and periods of strong equatorward winds. The weighted mean pigment image and the coefficient of variation image showed three clearly defined regions; a coastal region approximately 100 km wide, an offshore region of low pigment and low variability, and two filaments that extended several hundred kilometers offshore. Coastline topography and along shore variations in wind forcing are important in the coastal region. The offshore filaments appear to be related to the patterns of wind stress curl and perhaps explain the large-scale patterns of zooplankton biomass in the California Current. Analysis of the temporal variability delineated three nearshore areas: a northern region off Cape Mendocino, a central region near the CODE Central line, and a southern area off San Francisco. The width of the coastal zone seemed to vary with a 5- to 6-day cycle. During two equatorward

wind events, the patterns of temporal variability were consistent with the patterns of wind forcing revealed by empirical orthogonal function decomposition.  
Scripps Institution of Oceanography, A-002, La Jolla, CA 92093; Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Drive, Pasadena, CA 91109

4. Abel, R.B., *The role of satellites in ocean science and technology*, in *The Ocean in Human Affairs*, S.F. Singer, Editor. 1990, Paragon House: New York. p. 145-175.

A history and overview. Good and complete tables, together with predictions for future use.

5. Ackleson, S.G., J.J. Cullen, J. Brown, and M.P. Lesser. *Some changes in the optical properties of marine phytoplankton in response to high light intensity*. In *Ocean Optics X*. 1990. Orlando, FL 1302: p.238-249. SPIE.

In modeling the optical properties of and radiative transfer within ocean water, a common assumption is that the optical properties of the various dissolved and particulate constituents per unit concentration are constant. While this assumption is probably valid for non-living materials, it is frequently not the case with phytoplankton. Living cells are dynamic in their size, shape, and composition and respond readily to changes in the environment. Since each of these factors plays a role in determining the light scatter and absorption properties of the cell, the assignment of optical constants to phytoplankton cells may introduce significant errors in any theoretical treatment of radiative transfer and may result in erroneous interpretations of bulk optical measurements. In the case of phytoplankton exposed to high light intensities, variability in single-cell optical properties may occur as a result of cell swelling.

Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, ME 04575

6. Ackleson, G., *What happened during the 1989 Gulf of Maine coccolithophore bloom?* 1990, *Eos*, 71(2): p. 108.

In June, 1989, a coccolithophore bloom (species *Emiliana huxleyi*) formed within the southwestern portion of the Gulf of Maine. Bloom development was monitored with AVHRR visible band imagery. During the height of the bloom, a hydrographic survey was conducted to measure the optical, physical, and biological properties of the euphotic layer within and adjacent to the bloom. Microscopic examination of the water samples indicated that particulate material within the bloom was comprised almost entirely of *E. huxleyi* cells and detached coccoliths. Bulk optical properties at several wavelengths were measured: diffuse attenuation of downwelling irradiance, upwelling irradiance, beam attenuation, volume reflectance, and particulate absorption. These data were then combined with cell and coccolith counts, measurements of chlorophyll *a* concentration, nutrient concentrations and hydrographic data to investigate the effects of *E. huxleyi* optical properties on the euphotic layer. Preliminary analysis indicates that the euphotic layer within the bloom was affected in two ways as a result of light scatter from high concentrations of detached coccoliths. First, absorption by water and chlorophyll, enhanced by multiple scattering, resulted in a thinning of the euphotic layer within the coccolithophore bloom. Second, increased volume reflectance, due to backscatter from detached coccoliths, resulted in lower vertically integrated irradiance intensities.

Bigelow Laboratory for Ocean Science, West Boothbay Harbor, Maine 04575 (207 633 6326)

7. Alberte, R., A.M. Wood, T.K. Kursar and R.L. Guillard *Novel phycoerythrin in marine Synechococcus spp.: Characterization, and evolutionary and ecological implications*. *Plant Physiol.*, 1984. 75: p. 732-739.



Four clones of the marine, unicellular, cyanobacteria *Synechococcus* spp. were examined for the spectral and biochemical features of their phycoerythrins (PE) and their photosynthetic characteristics. Two spectral types of PE which are distinct from known PE's were found. One PE type possessed absorption maxima at 500 and 545 nm and a fluorescence emission at 560 nm. Upon denaturation in acid-urea, two chromophore absorption maxima were obtained, one corresponding to phycourobilin ( $A_{\max}$  500 nm) and one at 558 nm, ascribed to a phycoerythrobilin-like chromophore. The ratio of phycoerythrobilin-like to phycourobilin chromophores was 4.9:1.3. This PE possess two subunits of  $M_r$ s of 17.0 and 19.5 kD for the  $\alpha$  and  $\beta$  subunits, respectively. The other PE possessed a single symmetrical absorption at 551 nm and a fluorescence emission at 570 nm. This phycobiliprotein showed a single chromophore absorption band ( $A_{\max}$  558 nm) and yielded two polypeptides, an  $\alpha$  of 17.5 kD and a  $\beta$  subunit of 20.8 kD. Both PEs showed a  $(\alpha, \beta)_n$  structure. The presence of phycoerythrobilin-like chromophores ( $A_{\max}$  558 nm) appears to be diagnostic of this marine cyanobacterial group. The features of these PEs combined with additional biochemical data, suggest a possible evolutionary link between the PE-containing marine *Synechococcus* group and the red algal chloroplast. When the *Synechococcus* clones were grown under low light intensity, the PE-containing clones showed higher photosynthetic performance, larger photosynthetic units sizes, reaction center I to II ratios near unity, and steeper initial slopes of photosynthesis *versus* irradiance curves than a non-PE-containing clone. These findings demonstrate the high photosynthetic efficiency of PE-containing clones in low light environments common to middepth neritic and oceanic habitats. Barnes Laboratory, The University of Chicago, Chicago, IL 60637.

8. Alpine, A.E. and J.E. Cloern, *Differences in in vivo fluorescence yield between three phytoplankton size classes*. J. Plankton Res., 1985. 7(3): p. 381-390.

The size-dependent relationship between *in vivo* fluorescence (IVF) and chlorophyll *a* was determined for monthly phytoplankton samples from the San Francisco Bay estuary. Chlorophyll *a* and IVF were both measured in netplankton ( $>22 \mu\text{m}$ ), nanoplankton ( $5-22 \mu\text{m}$ ) and ultraplankton ( $<5 \mu\text{m}$ ) samples that were separated with screens. IVF and chlorophyll *a* were linearly related for each size class but the IVF per unit chlorophyll *a* (*R*) was significantly different between these three size classes. The ultraplankton *R* was twice that of the nanoplankton which was in turn twice the netplankton *R*. Hence, accurate size fractionation of phytoplankton biomass from measures of IVF requires correction for size-dependent variations in *R*.

U.S. Geological Survey MS496, 345 Middlefield Road, Menlo Park, CA 94025

9. Arnone, R.A., R.R. Bidigare, C.C. Trees, and J.M. Brooks, *Comparison of the attenuation of spectral irradiance and phytoplankton pigments within frontal zones*. In *Ocean Optics VIII*. 1986. Orlando, FL 637: p. 126-130. The International Society for Optical Engineering, SPIE, P.O. Box 10, Bellingham, WA 98227-0010.

Spectral irradiance and pigment (porphyrin and carotenoid) measurements were made across strong frontal boundaries of the Gulf Stream in the northwest Atlantic. Upwelling and downwelling irradiances were measured at 2 nanometer (2 nm) increments across the visible spectrum (400-700 nm). Pigment concentrations were determined by high performance liquid chromatography (HPLC). The irradiance spectra suggest that passive fluorescence occurs in frontal waters. The phytoplankton pigment composition showed significant changes across the frontal region. Pigment changes are reflected in the spectral attenuation coefficients, even at low pigment concentrations measured in Gulf Stream waters. Application of the spectral attenuation coefficient suggests an alternate method for accessing

the pigment character in surface waters. The surface pigment distribution aids in our understanding the ocean color variability measured with satellite sensors.  
Naval Ocean and Research Development Activity, NSTL, Mississippi 39529-5004

10. Arvesen, J.C., J.P. Millard, and E.C. Weaver. *Remote sensing of chlorophyll and temperature in marine and fresh waters*. Astronautica Acta., 1973. 18: p. 229-239.

An airborne differential radiometer was demonstrated to be a sensitive, real-time detector of surface chlorophyll content in water bodies. The instrument continuously measures the difference in radiance between two wavelength bands, one centered near the maximum of the blue chlorophyll *a* absorption region and the other at a reference wavelength outside this region. Flights were made over fresh water lakes, marine waters, and an estuary, and the results were compared with "ground truth" measurements of chlorophyll concentration. A correlation between output signal of the differential radiometer and the chlorophyll concentration was obtained. Examples of flight data are illustrated. Simultaneous airborne measurements of chlorophyll content and water temperature revealed that variations in chlorophyll are often associated with changes in temperature. Thus, simultaneous sensing of chlorophyll and temperature provides useful information for studies of marine food production, water pollution, and physical processes such as upwelling.  
Ames Research Center, NASA, Moffett Field, CA 94035

11. Arvesen, J.C., J.P. Millard, and E.C. Weaver. *Rapid assessment of water pollution by airborne measurement of chlorophyll content*. In *Joint Conference on Sensing of Environmental Pollutants*. 1971. Palo Alto, CA:

A method has been developed to remotely-sense the surface concentration and distribution of algae in water bodies by means of a differential radiometer which is sensitive to the spectral characteristics of chlorophyll. The algae serve as key indicators of the presence of inorganic nutrients, such as nitrogen and phosphorus, which stimulate algae growth and toxic materials, such as mercury compounds, DDT or endrin, which retard growth. Flights were performed to calibrate the instrumentation over various water bodies with a range of algae content. The instrumentation is capable of real-time continuous measurements of chlorophyll content over a range 0.01 to 10 mg/m<sup>3</sup>.  
Ames Research Center, NASA, Moffett Field, CA 94035

12. Atlas, D. and T.T. Bannister, *Dependence of mean spectral extinction coefficient of phytoplankton on depth, water color and species*. Limnol. Oceanogr., 1980. 25(1): p. 157-159.

From published absorption spectra of algae (green, blue-green, and diatoms) and from published data describing spectral irradiance as a function of depth in blue, green, and blue-green waters, values of the mean spectral extinction coefficient of the algae were calculated. For all three algal types, this value is nearly the same at the surface. For all three types, it increases with depth in blue water, decreases with depth in green water, and changes relatively little in blue-green water. The largest variation occurs with the green algae, ranging from 0.005 at depth in green water to 0.021 or more at depth in blue water, which means that the extinction coefficient varies as much as 4x.  
Dept. of Biology, University of Rochester, Rochester, NY 14627

13. Austin, R.W., *Coastal zone color scanner radiometry*. In *Ocean Optics VI SPIE*, S.Q. Duntley, Ed., 1979. Bellingham, WA 208: p. 170-177.

The characteristics of the Coastal Zone Color Scanner (CZCS) are described. The factors affecting the apparent radiance signature at the satellite are presented along with some representative examples of measured spectral radiances, irradiances and transmittances in the ocean and in the atmosphere. Finally an example is presented of the spectral

radiance components measured and computed for an experiment conducted in southern California coastal waters for the purpose of obtaining surface validation data at the time of a satellite overpass.

Visibility Laboratory, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093

14. Austin, R.W., *Gulf of Mexico, ocean-color surface-truth measurements*. Boundary-Layer Meteorology, 1980. 18: p. 269-285.

In October 1977, a major remote sensing experiment was conducted in the Gulf of Mexico, in preparation for the launch of NIMBUS-7 which carried the Coastal Zone Color Scanner. Two major vessels obtained surface-truth measurements, while two jet aircraft at altitudes of 12.5 and 19.5 km obtained images of the surrounding ocean in 10 spectral bands. Measurements obtained in the surface water from the NOAA vessel *Researcher* of the spectral downwelling irradiances, upwelling radiances, attenuation and scattering properties are described.

Visibility Laboratory, Scripps Institution of Oceanography, La Jolla, CA 92093

15. Austin, R.W. and T.J. Petzold, *The determination of the diffuse attenuation coefficient of sea water using the Coastal Zone Color Scanner*. In *Oceanography from Space*, J.F.R. Gower, Editor. 1981, Plenum Publishing Corporation: p. 239-256.

An algorithm is presented for deriving the diffuse attenuation coefficient (K) of sea water from the ratio of inherent upwelling radiances at 443 and 550 nanometers. *In situ* spectroradiometric data from 88 oceanographic stations taken by U.S., French and Japanese investigators working in a wide variety of water types were used to develop empirical relationships between the attenuation coefficient and the upwelling radiance (or irradiance) ratio. The relationships for estimating K's at 490 and 520 nm are presented along with the error of the estimate. Errors in the determination of K from *in situ* measurements are also discussed. Since the estimates of the inherent sea surface radiances can be derived from Coastal Zone Color Scanner (CZCS) data by using an appropriate atmospheric correction algorithm, a method thus exists for remotely assessing the optical properties of the surface waters of the ocean. By applying the above relationships to the inherent radiances calculated from the CZCS data, the attenuation coefficients for an entire CZCS scene may be rapidly obtained. An example is presented of an image representing the K(490) computed from CZCS data together with concurrent surface observations for comparison. The image shows the nature and scale of the variations of the optical properties of the coastal waters.

Visibility Laboratory, Scripps Institution of Oceanography, La Jolla, CA 92093

16. Austin, R.W. and T.J. Petzold, *Spectral dependence of the diffuse attenuation coefficient of light in ocean waters*. In *Ocean Optics VII*, M. Blizard, Ed., 1984. Bellingham, WA 489: p. 168-178. SPIE.

A study of the spectral nature of the diffuse attenuation coefficient of light,  $K(\lambda)$ , for various types of oceanic waters has been performed. These attenuation spectra were computed from downwelling spectral irradiance data,  $E_d(\lambda)$ , obtained by U.S., French and Japanese investigators, working in widely separated oceanic regions and using different measuring techniques and equipment. Attenuation properties were calculated over the spectral region from 365 to 700 nm and for depths from near surface to in excess of 100 meters. Examining the  $K(\lambda)$  data, we find strong, simple and useful relationships exist between the value of K at some selected wavelength,  $\lambda_0$ , and the value of K at some other wavelength such that  $K(\lambda) = M(\lambda) * [K(\lambda_0) - K_w(\lambda_0)] + K_w(\lambda)$ , where  $K_w$  is the attenuation coefficient for pure sea water. (Note:  $M(\lambda)$

is the slope of the regression line between  $K(\lambda)$  and  $K(490)$ .) For oceanic waters (for example Jerlov types I through III) the relationships are linear. These relationships appear to be useful throughout the entire spectral range examined and are particularly good between 420 and say 580 nm. The significance of the existence of such relationships is that they allow the inference of the spectral attenuation coefficient at all wavelengths from the attenuation value at a single wavelength, and provide analytical expressions for modeling the spectral nature of the attenuation in the ocean and clear coastal water.

Visibility Laboratory, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093

17. Austin, R.W. and T.J. Petzold. *Spectral dependence of the diffuse attenuation coefficient of light in ocean waters: A re-examination using new data*. In *Ocean Optics X*. 1990. Orlando, FL 1302: p. 79-85. SPIE.

A model devised earlier relating the spectral dependence of the attenuation coefficient for natural diffuse light in the ocean, to the value of the attenuation coefficient at a reference wavelength is re-examined using recently acquired data. These data are of uniformly high quality, and cover ocean latitudes from 24.4 to 77.4. An examination of the variation in the spectral  $K(\lambda)$  was prompted by a concern that the phytoplankton species distribution at high latitudes might differ sufficiently from that at tropical to mid-latitudes to require a change in the spectral  $K(\lambda)$  model. No change in the model is recommended on the basis of these findings.

Marine Resources Division, Scripps Institution of Oceanography, La Jolla, CA 92093.

18. Balch, W.M., M.R. Abbott, and R.W. Eppley, *Remote sensing of primary production - I. A comparison of empirical and semi-analytical algorithms*. Deep-Sea Research, 1989. 36(2): p. 281-295.

We evaluated several algorithms for their ability to predict integrated primary production using remotely sensed data. Published empirical algorithms and a previously unpublished algorithm were compared using data from the Southern California Bight Study and the California Cooperative Fisheries Investigation. The algorithms also were checked using satellite-derived chlorophyll measurements, and the predicted production then was compared to the shipboard-derived production estimate. A semi-analytical algorithm was derived that predicts production based on temperature and chlorophyll. Typically, the empirical algorithms account for about 25-38% of the variance in integral primary production. The performance of the empirical algorithms improved when satellite pigment data were used as input. The semi-analytical algorithm explained about 69% of the variance in surface production and 38% of the variance in integral production when shipboard data were used. The algorithm only explained 16-24% of the variance when satellite data were used. The explained variance in integral production could be increased to 44% by *in situ* "calibration" of the algorithm.

Division of Biology and Living Resources, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149-1098

19. Balch, W.M., R.W. Eppley, and M.R. Abbott, *Remote sensing of primary production - II. A semi-analytical algorithm based on pigments, temperature and light*. Deep Sea Research, 1989. 36(8): p. 1201-1217.

A semi-analytical algorithm for estimating integrated primary production is described which uses pigment, temperature and light data. The algorithm was designed using 648 stations of data from the California Cooperative Fisheries Investigation and the Southern California Bight Study. Pigment and temperature values were used to describe maximum photosynthesis in the surface waters. A model for the vertical distribution of chlorophyll was

devised which simplifies the estimation of those pigments too deep for the satellite to detect. Quantum yield, light utilization efficiency, and chlorophyll-specific light-utilization efficiency were described and parameterized for inclusion in the algorithm. Variance in the photosynthetic yield term was typically the largest. Some of the variance could be partitioned as nutrient effects and inter-cruise variability. Algorithm performance could be increased considerably by using one or two stations as "calibration" stations for each area of about 300,000 km<sup>2</sup> (and deleting such stations from subsequent analysis). Using ship data as input, the uncalibrated algorithm explained about 35% of the variance in primary production whereas the calibrated algorithm accounted for 58% of the variance. Using satellite data as input, the uncalibrated and calibrated algorithm accounted for 35 and 48% of the variance in primary production, respectively. Of the algorithms examined in Parts I and II of this series, the semi-analytical algorithm described here explains the most variance and comes the closest to a 1:1 ratio of predicted to observed production.

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20. Balch, W.M., *Primary production by satellite - Sharpening Occam's razor*, Aquatic Sciences Meeting, Am. Soc. Limnol. Oceanog., 1992, Santa Fe, NM.

The upcoming SeaWiFS mission will provide considerable information about chlorophyll and primary productivity in the marine environment. However, a current limitation is the accuracy of bio-optical algorithms. In this paper, I will use recently compiled sea truth data to test several pigment and productivity algorithms. The results show that elaborate models of photosynthesis do no better than simple three parameter models in predicting integral primary production, mainly due to the lack of knowledge about the photoadaptive parameters in space and time. The root of the problem lies in finding parameters besides pigment concentration that can be derived via satellite and that provide new information about primary production. Temperature is one such factor but previous attempts to apply temperature to productivity algorithms have only moderately improved accuracy. Reasons for this, as well as a possible solution will be discussed. In the oral presentation, Balch says that mixed layer depth can be determined from ocean color.

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21. Balch, W., R. Evans, J. Brown, G. Feldman, C. McClain, and W. Esaias, *The remote sensing of ocean primary productivity: Use of a new data compilation to test satellite algorithms*. J. of Geophysical Res., 1992. 97(C2 (Feb. 15, 1992)): p. 2279-2293.

We tested global pigment and primary productivity algorithms based on a new data compilation of over 12,000 stations occupied mostly in the northern hemisphere, from the late 1950's to 1988. The results showed high variability of the fraction of total pigment contributed by chlorophyll *a*, which is required for subsequent predictions of primary productivity. Two models, which predict pigment concentration normalized to attenuation length or euphotic depth, were checked against 2,800 vertical profiles of pigments (chlorophyll *a*, phaeopigment and total pigment). Phaeopigments consistently showed maxima at about one optical depth below the chlorophyll maxima. We also checked the global CZCS archive for data coincident with the sea truth data. A regression of satellite-derived pigment versus ship-derived pigment had a coefficient of determination of 0.40 (n=731 stations). The satellite underestimated the true pigment concentration in mesotrophic and oligotrophic waters (< 1mg pigment m<sup>-3</sup>) and overestimated the pigment concentration in eutrophic water (>1mg pigment m<sup>-3</sup>). The error in satellite estimate showed no trends with time between 1978 and 1985. In general the variability of the satellite retrievals increased with pigment

concentration. Several productivity algorithms were tested which utilize information on the photoadaptive parameters, biomass and optical parameters for predicting integral production. The most reliable algorithm which explained 67% of the variance in integral production for 1676 stations suggested that future success in deriving primary productivity from remotely sensed data will rely on accurate retrievals of "living" biomass from satellite data, as well as the prediction of at least one photoadaptive parameter such as maximum photosynthesis. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida 33149

22. Bannister, T.T., *Empirical equations relating scalar irradiance to  $a$ ,  $b/a$ , and solar zenith angle*. Limnol.Oceanogr., 1990. 35((1)): p. 173-177.

From Monte Carlo calculations, equations have been derived to predict underwater scalar irradiance as a function of depth, solar irradiance, and zenith angle at the surface, and absorption coefficient and ratio of scattering to absorption coefficients in the water. The equations correct for the depth dependence of the attenuation coefficient near the surface, and they predict scalar irradiance to within an error of <10%. Note:  $a$  is the volume absorption coefficient,  $b$  is the volume scattering coefficient.

Dept. of Biology, University of Rochester, Rochester, NY 14627.

23. Bannister, T.T., *Comparison of Kiefer-Mitchell and Bannister-Laws algal models*. Limnol. Oceanogr., 1990. 35(4): p. 972-979.

Kiefer-Mitchell model is simpler, and suffers from 3 categories of inaccuracies. But also, the Bannister-Laws model can neither be ruled in or out. Dept. of Biology, University of Rochester, Rochester, NY 14627

24. Banse, K. and C.R. McClain, *Winter blooms of phytoplankton in the Arabian Sea as observed by the Coastal Zone Color Scanner*. Mar.Ecol. (Prog. Ser.), 1986. 34(Dec. 19): p. 201-211.

Mean phytoplankton chlorophyll concentrations as estimated by the Nimbus-7 Coastal Zone Color Scanner are presented for 8 offshore areas of the Arabian Sea north of 10° N. Appreciable regional differences in levels and timing of changes of concentration were found, with large blooms being especially common in late winter north of about 20° N. Differences between the 2 autumn/winter periods in the timing of blooms were marked. Monthly means of surface water temperatures and winds did not provide explanations for the changes in pigment concentrations. Average chlorophyll concentrations north of about 20° N were significantly higher than those between about 10° and 15° N both prior to and during the months of seasonally elevated pigment levels. (Note: this article deals with a relatively enclosed marine area compared with the open ocean) Satellite values are far higher (up to 10x) than *in situ* values.

School of Oceanography, Seattle WB-10, University of Washington, Seattle, WA 98195 and NASA/Goddard Space Flight Center, Code 671, Greenbelt, MD 20771

25. Bartz, R., R.W. Spinrad, and J.C. Kitchen. *A low power, high resolution, in situ fluorometer for profiling and moored applications in water*. in *Ocean Optics IX*. 1988. Orlando, FL 925: p. 157-170. SPIE.

Sea Tech Inc. has developed an *in situ* fluorometer to measure chlorophyll  $a$  fluorescence in aquatic environments. The instrument has been developed within stringent constraints of size, weight and power consumption. The use of custom-designed components, including the flashlamp, excitation and emission filters, and energy storage capacitor for the light source has permitted optimal mechanical, optical and electrical design of the instrument. This new design results in efficient stimulation and detection of chlorophyll  $a$  fluorescence. The instrument is not sensitive to ambient light and has excellent stability over time and

temperature. Chlorophyll *a* concentration is measurable in three selectable ranges of approximately 3, 10 or 30  $\mu\text{g/l}$  full scale with a minimum detectable signal of  $<0.02 \mu\text{g/l}$ . Time constants of 0.1, 1, 3, and 10 seconds are selectable to smooth the output data. Power requirements are nominally 12 VDC at 150 mA, and output signal is 0 to 5 VDC. These power requirements and signal levels make the fluorometer compatible with most oceanographic moored and profiling data acquisition systems. Operating depth for the instrument is rated at 500 meters with a plastic housing or 3000 meters with a stainless steel pressure housing. SeaTech Inc., P.O. Box 779, Corvallis, OR 97339

26. Bidigare, R.R., M.C. Kennicut II, and J.M. Brooks, *Rapid determination of chlorophylls and their degradation products by high-performance liquid chromatography*. Limnol. Oceanogr., 1985. 30(2): p. 432-435.

A shipboard HPLC system is described which can provide quantitative determinations of chlorophylls *a*, *b*, *c*, and their degradation products. The technique is rapid ( $<20$  min), precise, and can detect chlorophyll *a* concentrations as low as 13 pg per injection. Representative data from the Southern Ocean are presented and briefly discussed. Dept. of Oceanography, Texas A&M University, College Station TX 77843

27. Bidigare, R.R., T.J. Frank, C. Zastrow, and J.M. Brooks, *The distribution of algal chlorophylls and their degradation products in the Southern Ocean*. Deep-Sea Res., 1986. 33(7A): p. 923-937.

Distributions of phytoplankton pigments were investigated in relation to temperature and optical variability along two 'long -line' transects in the Southern Ocean. Over 500 suspended particulate samples from 58 stations were analyzed for porphyrin pigment content using a shipboard high-performance liquid chromatography (HPLC) system. Both quantitative and compositional differences in algal pigments were observed along these transects. Variations in algal pigment concentrations were evident on scales of 200-500 km and appeared to be dependent on variations in physical hydrography along the cruise track. Chlorophyll *a* accounted for approximately half of the pigments measured, and the dominant accessory and degraded porphyrins were Chl *c* and phaeophorbide *a*, respectively. Physical processes and zooplankton grazing appear to be major factors controlling the summertime abundance of phytoplankton in the Southern Ocean. The usefulness of HPLC pigment analysis for investigating biological and optical variability in the marine environment is demonstrated.

Dept. Oceanogr. , Texas A & M, College Station, TX 77843

28. Bidigare, R.R., R.C. Smith, K.S. Baker, and J. Marra, *Oceanic primary production estimates from measurements of spectral irradiance and nutrient concentrations*. Global Biogeochemical Cycles, 1987. 1(3): p. 171-186.

A major objective of biological oceanography today is to quantify the mean and the variance of phytoplankton production on a global basis. Synoptic satellite sensing of the world's ocean is essential to this effort which requires contemporaneous sea surface data to provide complete water column information. Toward these objectives we present a spectrally dependent bio-optical model for the computation of *in situ* phytoplankton production. Using this model we show that *in situ* phytoplankton production can be accurately estimated from measurements of incident spectral irradiance and phytoplankton pigment concentrations. We also present estimates of photosynthetically absorbed radiation as a function of wavelength for a natural phytoplankton population. These complete spectral data provide insight into the wavelength-dependent utilization of radiant energy by phytoplankton and the influence of phytoplankton on the optical properties of the water column. We show that the model can be

used for shipboard observations and that it may be especially useful for predicting production rates from data provided by untended buoys.

Geochemical and Environmental Research Group, Texas A&M University, College Station 77943

29. Bidigare, R.R., J.H. Morrow, and D.A. Kiefer. *Derivative analysis of spectral absorption by phytoplankton pigments*. in *Ocean Optics IX*. 1988. Orlando, FL 925: p. 101-108. SPIE.

Concurrent measurements of the spectral absorption coefficient and photosynthetic pigmentation of natural particulates were performed to determine the principal pigments responsible for the absorption of spectral irradiance in seawater. The spectral absorption coefficient was analyzed by taking the second and fourth derivatives with respect to wavelength. The wavelength and magnitude of these derivative values provide useful information regarding the identification and quantification of phytoplankton pigments responsible for a given spectral signature. Linear relationships were examined and established between derivative values at selected wavelengths and concentrations of the major tetrapyrrole pigments, specifically chlorophylls *a*, *b*, and *c*. The method described here provides a rapid means of obtaining estimates of photosynthetic pigment concentrations in natural samples where absorption can be strongly influenced by detrital matter.

Bidigare is at Texas A&M University, College Station, Texas 77843; Kiefer is at University of Southern California, Dept. of Biological Sciences, Los Angeles, CA 90089-0371

30. Bidigare, R.R., J.H. Morrow, and D.A. Kiefer, *Derivative analysis of spectral absorption by photosynthetic pigments in the western Sargasso Sea*. J. Mar. Res., 1989. 47(2): p. 323-341.

Concurrent measurements of the spectral absorption coefficient and photosynthetic pigmentation of natural particulates were performed to determine the principal pigments responsible for the absorption of spectral irradiance in seawater. The spectral absorption coefficient,  $A_p(\lambda)$ , was then analyzed by taking the second and fourth derivatives with respect to wavelength. The wavelength and magnitude of these derivative values provide useful information regarding the identification and quantification of phytoplankton pigments responsible for a given spectral signature. Linear relationships were examined and established between derivative values at selected wavelengths and concentrations of the major tetrapyrrole pigments, specifically chlorophylls *a*, *b*, and *c*. The correlation between derivative values near 526 nm and concentrations of photosynthetic carotenoids was poor and presumably caused by the broad absorption spectra of these pigments. A comparison of the measured particulate absorption coefficient with the absorption coefficient "reconstructed" for the phytoplankton component revealed that detritus can be a major source of light absorption. The method described here provides a rapid means of obtaining estimates of photosynthetic pigment concentrations in natural samples where absorption can be strongly influenced by detrital matter.

Geochemical and Environmental Research Group, Texas A&M University, College Station, Texas, 77843

31. Bidigare, R.R., D. Schofield, and B.B. Prezelin, *Influence of zeaxanthin on quantum yield of photosynthesis of Synechococcus clone WH7803 (DC2)*. Mar. Ecol. (Prog. Ser.), 1989. 56(1-2): p. 177-188.

*Synechococcus* clone WH7803(DC2) was grown on a 12:12 h light-dark cycle of either blue-green fluorescent, white fluorescent or daylight-filtered tungsten light. Integrated irradiance for each culture was set at  $15 \mu\text{E m}^{-2}\text{s}^{-1}$ . Subsequent measurements of absorption, pigmentation and carbon action spectra were used to examine wavelength-dependence



of photosynthetic quantum yield. Comparison of directly-measured and reconstructed absorption spectra suggests that pigment packaging effects are minimal in *Synechococcus*. Spectral quality had a marked effect on pigmentation and quantum yield. Cellular concentrations of chlorophyll *a*,  $\beta$ -carotene and phycoerythrin were all ~2-fold lower in daylight-grown *Synechococcus* relative to blue-green and white light-grown cells; ratios of  $\beta$ -carotene- and phycoerythrin-to-chlorophyll *a* were markedly constant for all 3 illuminations. Blue-green light grown *Synechococcus* cells had a ~2-fold higher zeaxanthin content than those grown under white light or daylight illuminations. These results indicate that cellular zeaxanthin content is not an implicit constant and its concentration is dependent on irradiance levels of blue-green light. Zeaxanthin probably serves an important function as a photoprotectant pigment in *Synechococcus*, and as such, can also produce significant decreases (20 to 40%) in the apparent quantum yield for photosynthesis in the blue-green region of the visible spectrum. In contrast, highest quantum yields were routinely measured between 525 and 650 nm suggesting that light absorbed by phycobilins (phycocyanin and phycoerythrin) drive the majority of carbon fixation in DC-2-like coccoid cyanobacteria. In calculating the spectral quantum yield for natural phytoplankton populations, it is suggested that (1) carbon action spectra be determined under 'enhanced' conditions and (2) photosynthetically absorbed radiation for phytoplankton be estimated using spectral reconstruction techniques where absorption contributions by non-photosynthetic chromophores are removed from whole cell absorption signatures.

Geochemical and Environmental Research Group, Dept. Oceanography, Texas A&M Univ., College Station, TX 77843

32. Bidigare, R.R., J. Marra, T.D. Dickey, R. Iturriaga, K.S. Baker, R.C. Smith, and H. Pak, *Evidence for phytoplankton succession and chromatic adaptation in the Sargasso Sea during spring 1985*. Mar. Ecol. (Prog. Ser.), 1990. 60(1-2): p. 113-122.

Measurements of photosynthetic pigments, nutrients, spectral irradiance and various physical parameters were performed in the western Sargasso Sea (35° N, 70° W) to investigate the factors affecting phytoplankton biomass distributions. Algal pigment concentrations and compositions measured during spring 1985 showed considerable time-dependent variations which were consistent with those documented by direct microscopic observation. During early April, 2-fold increases in chlorophyll *a* and fucoxanthin were measured in a relatively short time scale of days. The presence of a diatom-dominated community, mainly species of the genera *Rhizosolenia* and *Chaetoceros*, suggested that we were witnessing a stage of the spring bloom. Upon return to this location 2 weeks later, the diatom bloom was replaced by a considerably more diverse phytoplankton assemblage consisting of prymnesiophytes, cyanobacteria, dinoflagellates, green algae (including prasinophytes) and diatoms. The vertical structures displayed by individual accessory pigments during April were markedly similar and suggest that the major phytoplankton taxa were not uniformly distributed in the upper 200 m. The phytoplankton were distributed in broadly overlapping layers, with cyanobacteria and diatoms most abundant in the mixed layer, prymnesiophytes at intermediate depths, and green algae (including prasinophytes) deeper in the water column. Results provide descriptive evidence for a rapid succession of chromatically-adapted phytoplankton during springtime in the Sargasso Sea.

Dept. Oceanography. Texas A&M University, College Station, TX 77843 (Bidigare)

33. Bidigare, R.R., M.C. Kenicutt, M.E. Ondrusek, M.D. Keller, and R.R.L. Guillard, *Novel chlorophyll-related compounds in marine phytoplankton: Distributions and geochemical implications*. Energy & Fuels (originally presented at ACS Symposium on Porphyrin Geochemistry - the Quest for Analytical Reliability. E.I. Conf. No. 13979), 1990. 4: p. 653-657.

The distribution of chlorophyll-related pigments in marine phytoplankton is surveyed to document their occurrence, re-evaluate their use as biological markers, and suggest precursor-geoporphyrin relationships. Newly identified chlorophyll *c*-related pigments were widely distributed among the marine phytoplankton clones examined in this study. Two of the recently described chlorophyll *c*-like pigments (chlorophyll *c3* and a phytylchlorophyll *c* derivative) were found to be associated with common bloom-producing chromophytes, thus having potential for preservation in the sedimentary record. The taxonomic specificity and apparent geological stability of chlorophyll pigments suggest that geoporphyrins are excellent candidates as indicators of paleoceanographic/depositional environments. The high structural diversity observed among geoporphyrins may be explained by the complexity of precursor pigments found in marine phytoplankton and bacterioplankton and not by extensive diagenetic transformations. The introduction of methods providing greater resolution (liquid chromatography/mass spectrometry and supercritical fluid chromatography/mass spectrometry) of complex chlorophyll mixtures and specific detection should lead to the discovery of an even more diverse collection of chlorophyll pigments.

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34. Bidigare, R.R., M.E. Ondrusek, J.H. Morrow, and D.A. Kiefer, *In vivo absorption properties of algal pigments*. in *Ocean Optics X*. 1990. Orlando, FL 1302: p. 290-302. SPIE.

Estimates of the *in vivo* absorption coefficients ( $\text{m}^2 \text{mg}^{-1}$ , 400-750 nm, 2 nm intervals) for the major algal pigment groups (chlorophylls, carotenoids and phycobilins) are presented. "Unpackaged" absorption coefficients were initially obtained by measuring the absorption properties of pure pigment standards spectrophotometrically and "shifting" their absorption maxima to match *in vivo* positions. Two approaches for estimating the phytoplankton absorption coefficient (spectral reconstruction and spectral decomposition) are compared by linear regression analysis, incorporating concurrent measurements of particulate absorption and pigmentation performed in the Sargasso Sea. Results suggest that "pigment package" effects are minimal for natural assemblages of open-oceanic phytoplankton and that accessory pigments do not always co-vary with chlorophyll *a* over time. (Note: No information on extracted phycoerythrin, nor method to extract, and no mention of phycocyanin.)

Geochemical and Environmental Research Group, Dept. of Oceanography, Texas A&M University, College Station, Texas 77843

35. Bidigare, R.R. and M.E. Ondrusek, *Seasonal variation in phytoplankton pigmentation and absorption properties at Site L (34°N, 70°W)*. *Eos*, 1990. 71: p. 108.

Knowledge of the mean and variances of "photosynthetically absorbed radiation" in the upper ocean is critical for the construction of bio-optical models which accurately predict carbon fixation rates of marine phytoplankton. Toward this goal, suspended particulate samples were collected from the upper 200 m at Site L (34°N, 70°W) to investigate seasonal and depth dependent variations in phytoplankton pigmentation and absorption properties. The quantitatively important acetone-extractable pigments were chlorophylls *a*, *b*, *c*, 19'-hexanoyloxyfucoxanthin, 19'-butanoyloxyfucoxanthin, and zeaxanthin, reflecting the importance of prymnesiophytes, crysophytes, "green" algae and cyanobacteria as algal biomass components at Site L. Good agreement was observed between the distribution of zeaxanthin and cyanobacteria counts. For the minor xanthophylls measured, prasinoxanthin (prasinophyte marker) and alloxanthin (cryptophyte marker) were most abundant during late fall and winter; peridinin (dinoflagellate marker) concentrations were higher during summer. A distinct layering of the pigments was evident during stratified water column conditions. Corresponding variations in phytoplankton absorption properties were assessed using spectral reconstruction techniques and discussed in relation to the chromatic adaptive behavior.

36. Blizard, M.A. *Ocean optics: Introduction and overview*. in *Ocean Optics VIII*. 1986. Orlando, FL 637: p. 2-17. SPIE.

This paper provides an introduction and overview of the discipline known as "ocean optics". Emphasis is on basic concepts, the optical quantities involved, their measurement, and interconnecting theoretical relationships. Specific topics include radiometric properties, inherent optical properties, apparent optical properties, effect of bandwidth on Gershun's Law, measuring the volume scattering function, effect of the deep chlorophyll layer, removal of cloud effects from depth profiles of irradiance, and future directions.

Office of Naval Research, Arlington, VA 22217. SPIE address is: P.O. Box 10, Bellingham, WA 98227-7053. Tel: 206/676-3290

37. Blizard, M.A. *Ocean optics: Introduction and overview-1988*. in *Ocean Optics IX*. 1988. Orlando, FL 925: p. 2-11. SPIE.

This paper provides an introduction and overview of the discipline known as "ocean optics". Emphasis is on basic concepts, the optical quantities involved, their measurement, and inter-connecting theoretical relationships. Topics include radiometric quantities, inherent optical properties, apparent optical properties, measuring the spectral absorption coefficient, measuring the volume scattering function, effect of the deep chlorophyll layer, and future directions.

Office of Naval Research, Arlington, VA 22217

38. Boczar, B.A. and B.B. Prezelin *The organization of chlorophyll in marine dinoflagellates*. J. Phycol. 1985 (abstract #64 for the Annual Meeting of Phycological Society of America, Gainesville, Florida) 21: p. 14.

Previous investigators have successfully isolated two major pigment-protein complexes from the marine dinoflagellates, *Glenodinium* sp. and *Gonyaulax polyedra*: the light-harvesting peridinin-chl *a*-protein (PCP) complex, and a P700-chl *a*-protein complex. Using SDS solubilization and Deriphat-PAGE techniques, it has now been possible to further isolate at least four unique chlorophyll-protein complexes from the thylakoid membranes of these organisms: complex I, spectrally similar to the P700-chl *a*-protein complex; complex II, a unique chl *a*-chl *c* protein complex; and complexes III and IV, components of the PCP complement that are closely associated with the thylakoid membrane. Changes in the distribution of chlorophylls among these complexes occurred when *Glenodinium* sp. or *Gonyaulax polyedra* cells were grown under high irradiances; these changes reflected changes in cellular chlorophyll concentrations that occurred during photoadaptation.

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39. Booth, B.C., *The use of autofluorescence for analyzing oceanic phytoplankton communities*. Bot. Mar., 1987. 30: p. 101-108.

A simple cryo-preservation method of preparing phytoplankton samples for epifluorescence microscopy allowed observation of autofluorescence of 52 species of nano- and picoplankton after storage periods of 6 months and longer. Samples were fixed in glutaraldehyde, concentrated at sea using filtrations, and stored in oil at -15 C. Using this method, cell counts of field populations of *Synochococcus* spp. and larger phototrophs made after 2 years of storage were not significantly different from counts made on the day of collection. Most of the species of nanoplankton tested were destroyed by fixation in formalin. Lugol's fixative was the gentlest preservative tested but inappropriate for epifluorescence

microscopy. Glutaraldehyde caused shrinkage of cell diameters of *ca.* 13% and (when combined with critical point drying) shrinkage of *ca.* 40%.  
School of Oceanography. WB-10., University of Washington, Seattle, Washington 98195

40. Borstad, G.A. and D.A. Hill. *Using visible range imaging spectrometers to map ocean phenomena*. in *Proc. Advanced Optical Instrumentation for Remote Sensing of the Earth's Surface from Space*. 1989. Paris, France 1129: p. 130-136. SPIE.

Recent developments in remote sensing technology using two dimensional array detectors have resulted in a growing family of sensors called imaging spectrometers. Two instruments built in Canada have the very high spectral resolution and sensitivity required to image water color variations due to such phenomena as the blue-green absorption of certain fish and of marine plants, and the solar stimulated *in vivo* fluorescence from the chlorophyll pigment molecule. This paper briefly describes the Fluorescence Line Imager (FLI), built in 1983 for the Canadian Department of Fisheries and Oceans, and a smaller, more flexible, second generation instrument called the Compact Airborne Spectrographic Imager (CASI), first tested in the summer of 1988. Examples of spectral and spatial image data over a number of different targets are shown and the use of this technology for mapping coastal sites is discussed.

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41. Borstad, G.E., D.A. Hill, and R.C. Kerr. *Use of the Compact Airborne Spectrographic Imager (CASI): laboratory examples*. in *Proc. 12th Canadian Symposium on Remote Sensing*, 1989. IGARSS. Digest: p. 2081-2084.

As more and more remote sensing applications are found requiring high spectral resolution, there is a need for a small, easy to use instrument designed for experimental projects. The Compact Airborne Spectrographic Imager (CASI) is a newly developed, second generation imaging spectrometer for use in small aircraft or in the laboratory. The CASI operates in the 423-946 nm spectral range with 288 spectral bands, has a variable field of view depending on the fore-optics, 12-bit dynamic range and 2.2 Gbyte recording capacity on digital cassette tape. Power consumption is 250 Watts, 110 Hz. The system has a real time display of one spatial (image) band and one spectral channel and an interactive, menu-driven control. The 288 spectral bands are co-registered with a single 'track recovery image' which allows high accuracy in determining the ground location of spectral data. This paper describes the user interface during data acquisition, and reviews and discusses the philosophy of spectral data handling.

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(604)656-5633.

42. Brewer, P.G., K.W. Brewer, R.W. Eppley and J.J. McCarthy, *The global ocean flux study (GOFS): Status of the U.S. GOFS program*. *Eos*, 1986. 67(44): p. 827-832.

The early prototype satellite (the Coastal Zone Color Scanner or CZCS) that has now delivered the first essential glimpse of global pigment data faces system failure and must be replaced by successor instruments. GOFS can be accomplished through a combination of sophisticated research cruises, satellite ocean color observations, moored and drifting instrumentation of novel design, and advanced numerical modeling and data assimilation techniques. It will require genuine and vigorous international cooperation for a decade or more. Woods Hole Oceanographic Institution, Woods Hole, MA (Brewer now directs MBARI in Pacific Grove, CA)

43. Brown, C.W. and J.A. Yoder. *Global distribution pattern of coccolithophore blooms.*, Aquatic Sciences Meeting, Am. Soc. Limnol. Oceanog., 1992. Santa Fe.

The location of surface coccolithophore blooms in the world's oceans was mapped by applying a supervised classification scheme to weekly global composites of coastal zone color scanner (CZCS) imagery dating from 1978 to 1986. Blooms were spectrally distinguishable from other water conditions due to their high reflectance of light at CZCS band wavelengths. In the northern hemisphere, in addition to the previously reported occurrence of blooms to the south of Iceland and in the vicinity of the United Kingdom and Newfoundland, blooms were observed in pelagic waters east of Newfoundland, on the Norwegian continental margins, in the Baltic and Black Seas and in the Northwest Pacific Basin off Japan between May to October, and in the Persian Gulf between January and February. In the southern hemisphere, blooms occurred in the Arafura Sea of northern Australia between May and July, and along the Argentine Basin shelf break and at two sites in the Southern Ocean (~105° W, 60° S and 25° E, 60° S) between January and March.

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44. Bukata, R.P., J.H. Jerome, J.E. Bruton, S.C. Jain, and H.H. Zwick, *Optical water quality model of Lake Ontario. 1: Determination of the optical cross sections of organic and inorganic particulates in Lake Ontario*. Applied Optics, 1981. 20(9): p. 1696-1703.

A five-component optical model of Lake Ontario is discussed in terms of unique organics (as represented by chlorophyll *a*), unique inorganics (as represented by total suspended minerals), unique nonliving organics and unique dissolved organics. Direct measurements of the irradiance attenuation coefficient and the diffuse reflectance and the total attenuation coefficient are used in conjunction with simulated solutions of the radiative transfer equations to determine the inherent optical properties of the water mass. Multiple regressions between these inherent optical properties and directly measured water quality data are then performed to determine the absorption, scattering, and backscattering cross sections of the organic and inorganic components.

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45. Bukata, R.P., J.E. Bruton, J.H. Jerome, S.C. Jain, and H.H. Zwick, *Optical water quality model of Lake Ontario. 2: Determination of chlorophyll *a* and suspended mineral concentrations of natural waters from submersible and low altitude optical sensors*. Applied Optics, 1981. 20(9): p. 1704-1714.

Spectroscopical and water quality data collected from a 1979 coordinated *in situ* and airborne study of western Lake Ontario are used to devise a five-component model from which subsurface chlorophyll *a* and suspended solids concentrations may be determined from submersible optical sensors capable of measuring spectral irradiance reflectance just beneath the free-surface layer. A water-air interface model, which incorporates the effects of surface reflection, is also presented in an attempt to extend such water quality estimations to low altitude remote sensors. Special emphasis is given to the spectral wavelength bands of the Coastal Zone Color Scanner aboard Nimbus-7.

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46. Bukata, R.P., J.H. Jerome, K.Y. Kondratyev, and D.V. Pozdnyakov, *Estimation of organic and inorganic matter in inland waters: optical cross sections of Lakes Ontario and Ladoga*. J. Great Lakes Res., 1991. 17(4): p. 461-469.

The high degree of optical complexity of inland water masses necessitates the development of models which consider the optical competitiveness of several co-existing aquatic components. A model is described which was developed to simultaneously estimate chlorophyll *a*, suspended mineral, and dissolved organic carbon concentrations from a single

measurement of the subsurface volume reflectance spectrum in the optically complex waters of Lake Ontario. To estimate such aquatic concentrations requires a quantification, as a function of wavelength, of the amount of scattering and absorption that may be ascribed to a unit concentration of each aquatic component (i.e. the pertinent optical cross sections). Cross section spectra are presented for Lake Ontario and it is illustrated how such cross sections may be utilized in conjunction with directly-measured subsurface volume reflectance spectra and optimization analyses to extract the organic and inorganic components. Cross section spectra obtained in a similar manner for Lake Ladoga are also presented and compared to those of Lake Ontario. Similarities in absorption, but differences in backscattering cross section spectra for suspended inorganic matter were observed for the two lakes. Near-identical absorption and very similar backscattering cross section spectra suggest that Lakes Ontario and Ladoga are characterized by optically-comparable populations of chlorophyll-bearing biota.

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47. Bukata, R.P., J.H. Jerome, K.Y. Kondratyev, and D.V. Pozdnyakov, *Satellite monitoring of optically-active components of inland waters: an essential input to regional climate change impact studies*. J. Great Lakes Res., 1991. 17(4): p. 470-478.

Consistent with the climate change objectives of the IGPB (International Geosphere-Biosphere Program) is the need to remotely monitor and map both global and regional biological productivity over lands, oceans, and inland waters. Models and algorithms are currently being developed to infer aquatic primary production from near-surface chlorophyll concentration values determined from satellite sensors. Data from Lake Ladoga are utilized to illustrate that the algorithms currently being used to monitor near-surface chlorophyll concentrations in oceanic waters are inadequate when applied to water masses optically complicated by their proximity to land masses. Methodologies originally developed for retrieving simultaneous concentrations of chlorophyll, suspended minerals, and dissolved organic carbon from volume reflectance measurements of Lake Ontario are shown to display success in Lake Ladoga that could not be duplicated by six different oceanic chlorophyll retrieval algorithms. The principal requirements for water quality satellite monitoring are the cross-sections of the optically-active components of the water body being remotely monitored. It is argued that, despite the spatial and temporal variability of such cross sections, their determination for principal water bodies should comprise both global and regional climate change studies.

National Water Research Institute, Canada Centre for Inland Waters, Box 5050, Burlington, Ontario L7R 4A6 and Institute for Lake Research, Russian Academy of Sciences, St. Petersburg, Russia.

48. Carder, K.L. and R.G. Steward, *A remote sensing reflectance model of a red-tide dinoflagellate off west Florida*. Limnol. Oceanogr., 1985. 30: p. 286-298.

A mathematical model that simulates the spectral curves of remote-sensing reflectance of blooms of the red-tide dinoflagellate *Ptychodiscus brevis* is developed. The model is compared to measurements obtained from a low-flying helicopter for *P. brevis* populations with chlorophyll-like pigment concentrations from 7 to 77 mg m<sup>-3</sup> found in case 2 waters along the west Florida shelf in October 1983. The model simulates the effects of backscattering from water, phytoplankton, detritus, and yellow dissolved matter ("Gelbstoff") for case 1 and case 2 waters. It can be easily modified to simulate the spectral reflectance of phytoplankton from other pigment color groups. Matching the model spectral curves to measured remote-sensing reflectance curves provides accurate estimates of chlorophyll *a* plus pheophytin *a* and also

estimates of Gelbstoff and detritus concentrations. Comparison of remote-sensing reflectance data to model reflectance data allows calculation of the quantum efficiency of fluorescence for a given phytoplankton population, which provides a remote measurement of a factor that has been found to increase with the nutrient stress of the population.

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49. Carder, K.L., R.G. Steward, J.H. Paul, and G.A. Vargo, *Relationships between chlorophyll and ocean color constituents as they affect remote-sensing reflectance models*. Limnol. Oceanogr., 1986. 31(2): p. 403-413.

Good agreement between satellite-derived and shipboard measurements of chlorophyll *a* + pheophytin *a* concentrations results from the covariance of each of the non-water color constituents of the ocean with pigment concentration. The specific absorption coefficient at 440 nm varies directly with the submicron chlorophyll fraction, which itself varies inversely with total chlorophyll concentration. Both the backscattering coefficient for particles and the Gelbstoff absorption coefficient increase with chlorophyll pigments. An analytical remote-sensing reflectance model for chlorophyll concentrations in the eastern Gulf of Mexico is developed from these relationships and tested against an independent data set. By this approach, remote-sensing algorithms can be developed that respond to regional and seasonal differences in runoff (e.g. terrigenous Gelbstoff and detritus), phytoplankton size, and pigment color groups.

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50. Carder, K.L., D.J. Collins, M.J. Perry, H.L. Clark, J.M. Mesias, J.S. Cleveland and J. Greenler. *The interaction of light with phytoplankton in the marine environment*. in *Ocean Optics VIII*. 1986. Orlando, FL 637: p. 42-55.

In many regions of the ocean, the phytoplankton population dominates both the attenuation and scattering of light. In other regions, non-phytoplankton contributions to the absorption and scattering may change the remote sensing reflectance and thus affect our ability to interpret remotely sensed ocean color. Hence, variations in the composition of both the phytoplankton population and of the non-phytoplankton material in the water can affect the optical properties of the sea. The effects of the contributions to the remote sensing reflectance and the submarine light field are modeled using scattering and absorption measurements of phytoplankton cultures obtained at the Friday Harbor laboratory of the University of Washington. These measurements are used to develop regional chlorophyll algorithms specific to the summer waters of Puget Sound for the Coastal Zone Color Scanner, Thematic Mapper, and future Ocean Color Imager., and their accuracies are compared for high chlorophyll waters with little or no Gelbstoff, but with variable detrital and suspended material.

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51. Carder, K.L., R.G. Steward, R.F. Chen, S. Hawes, and Z. Lee, *AVIRIS calibration and application in coastal oceanic environments: tracers of soluble and particulate constituents of the Tampa Bay coastal plume*. Photogramm. Engineer. Rem. Sens., 1993. 59(3): p. 339-344.

AVIRIS is a test-bed for future spacecraft sensors such as HIRIS and MODIS planned for the Earth Observing System. Model-derived absorption coefficients at 415 nm,  $a(415)$ , and back-scattering coefficients at 671 nm,  $b_b(671)$ , for Tampa Bay waters were used to create images from AVIRIS data of the dissolved component of  $a(415)$  due to gelbstoff,  $a_g(415)$ , and salinity. Images of  $a_g(415)$ , salinity, and  $b_b(671)$  were used to depict the

distribution of dissolved and particulate constituents, respectively, for Tampa Bay plume during late, ebb-tidal conditions. Salinity covaried with  $a_g(415)$ , which provided a means of mapping salinity from the  $a_g(415)$  imagery. The concentration of suspended particles as inferred from  $b_b(671)$  was extremely variable in the shallow regions where waves and currents interacted. Pollutants covarying with fresh water or suspended sediments can be mapped from  $a_g(415)$  and  $b_b(671)$  images, respectively.

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52. Chamberlin, W.S., C.R. Booth, D.A. Kiefer, J.H. Morrow, R.C. Murphy. *Evidence for a simple relationship between natural fluorescence, photosynthesis and chlorophyll in the sea*. Deep Sea Res., 1990. 36(6): p. 951-973.

To test the proposal that the natural or solar-induced fluorescence of chlorophyll *a* in the sea provides a purely optical measure of chlorophyll and the rate of photosynthesis in the sea, we studied the relationship between natural fluorescence and photosynthesis in several environments including the central South Pacific, the western Sargasso Sea, and two sheltered bays. The results of 76 such measurements between 2 and 150 m depth and covering a 1500-fold range in production indicate that photosynthesis is highly correlated ( $r > 0.9$ ) with natural fluorescence. Furthermore, a substantial portion of the remaining variability can be explained by an examination of the relationships of the quantum yields of photosynthesis and fluorescence as a function of light level. Specifically, the quantum yield of photosynthesis decreases more rapidly than the quantum yield of natural fluorescence with increasing irradiance. Predicted rates of primary production from measures of natural fluorescence and PAR fall within  $\pm 30\%$  for half the samples, and within  $\pm 75\%$  for 90% of the cases (assuming that the carbon fixation measurements were without error). The prediction of chlorophyll from natural fluorescence and PAR exhibit similar correlations. This suggests that natural fluorescence measurements, either as a supplement to direct measurements or as independent optical measurements, provide a new and rapid means of estimating gross photosynthesis in the sea. (Note: natural fluorescence, emitted as a narrow band centered at 683 nm, is strongly absorbed by water. Also, the fluorescence yield of chlorophyll is low in cyanobacteria, because most of the chlorophyll is found in the antenna of photosystem 1 which is not fluorescent. Thus we expect that the ratio of photosynthetic yield to fluorescence yield will be much higher for species of *Synechococcus* than for the eucaryotic species of photosynthetic plankton.)

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53. Chamberlin, W.S., J. Marra, R.A. Reynolds, D.A. Keifer, and C.R. Booth, *Consideration of factors which affect the relationship between photosynthesis and natural fluorescence*. 1990, Eos, 71: p. 108.

Recent experiments in the Sargasso Sea, the South Pacific Ocean, and Weddell-Scotia Sea, and the North Atlantic Ocean are reviewed with consideration of factors which affect the relationship between natural fluorescence and photosynthesis. Although a satisfactory relationship has been found between these two quantities, the data indicate that light-, nutrient-, and/or temperature-dependent effects may be important. In particular, the ratio of the quantum yields of photosynthesis and natural fluorescence appears to be a function of light intensity, the ratio decreasing at high light intensities. Data from the Weddell-Scotia Seas indicate a higher quantum yield of natural fluorescence than observed in other oceans. We postulate that this effect is due to low temperature. Laboratory data on steady-state cultures of marine phytoplankton provide further evidence of light- and nutrient-dependent effects on the ratio of the quantum yields.



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54. Cheng, R.T. *Modeling of tidal and residual circulation in San Francisco Bay, California*. in *Two-Dimensional Flow Modeling*. 1982. Davis, CA: U.S. Army Corps of Engineers.

A team of research scientists in the U.S. Geological Survey uses the San Francisco Bay system as an outdoor laboratory to study the complex interactions between physical, chemical and biological processes which take place in estuarine systems. The broad goals are to understand processes and rates by which water, solutes, sediments, and organisms interact. Water circulation plays an important role in these ecological interactions; careful interfacing of hydrodynamic models with biological and chemical models will be most useful. Project Chief, Water Resources Division, USGS, Menlo Park, CA 94025

55. Cheng, R.T. and V. Casulli, *On Lagrangian residual currents with applications in South San Francisco Bay, California*. Water Resources Research, 1982. 18(6): p. 1652-1662.

The Lagrangian residual circulation has often been introduced as the sum of the Eulerian residual circulation and the Stokes' drift. Unfortunately, this definition of the Lagrangian residual circulation is conceptually incorrect because both the Eulerian residual circulation and the Stokes' drift are Eulerian variables. In this paper a classification of various residual variables is reviewed and properly defined. The Lagrangian residual circulation is then studied by means of a two-stage formulation of a computer model. The tidal circulation is first computed in a conventional Eulerian way, and then the Lagrangian residual circulation is determined by a method patterned after the method of markers and cells. To demonstrate properties of the Lagrangian residual circulation, application of this approach in South San Francisco Bay, California, is considered. With the aid of the model results, properties of the Lagrangian residual circulation from Eulerian data may lead to unacceptable error, particularly in a tidal estuary where the tidal excursion is of the same order of magnitude as the length scale of the basin. A direction calculation of the Lagrangian residual circulation must be made and has been shown to be feasible.

US Geological Survey, Menlo Park, CA 94025

56. Chisholm, S.W., R.J. Olson, E.R. Zettler, R. Goericke, J.B. Waterbury, and N.A. Welschmeyer. *A novel free-living prochlorophyte abundant in the oceanic euphotic zone*. Nature, 1988. 334: p. 340-343.

The recent discovery of photosynthetic picoplankton has changed our understanding of marine food webs. Both prokaryotic and eukaryotic species occur in most of the world's oceans and account for a significant proportion of global productivity. Using shipboard flow cytometry, we have identified a new group of picoplankters which are extremely abundant, and barely visible using traditional microscopic techniques. These cells are smaller than the coccoid cyanobacteria and reach concentrations greater than  $10^5$  cells per ml in the deep euphotic zone. They fluoresce red and contain a divinyl chlorophyll *a*-like pigment, as well as chlorophyll *b*, *alpha*-carotene, and zeaxanthin. This unusual combination of pigments, and a distinctive prokaryotic ultrastructure, suggests that these picoplankters are free-living relatives of *Prochloron*. They differ from previously reported prochlorophytes - the putative ancestors of the chloroplasts of higher plants - in that they contain *alpha*-carotene rather than *beta*-carotene and contain a divinyl chlorophyll *a*-like pigment as the dominant chlorophyll. 48-425 Massachusetts Institute of Technology, Cambridge, MA 02139

57. Cleveland, J.S., W.S. Chamberlin, J.H. Morrow, R. Iturriaga, R.R. Bidigare, M.J. Perry, and D.A. Siegel. *Estimation of the phytoplanktonic component of particulate light absorption: An evaluation of approaches*. Eos, 1990. 71(2): p. 109.

Measurements of the light absorbed by phytoplankton are needed for various oceanographic applications, but the population of light-absorbing particles in the ocean includes many other particle types. As part of the Biowatt program, several techniques for estimating the absorption of phytoplankton, independent of other particles, have been developed. These approaches include partitioning total particulate absorption based on shapes (not magnitudes) of phytoplankton absorption spectra; multiple regression analysis based on  $a(570)$  and  $a(675)$ ; microphotometry of individual particles; reconstruction from HPLC-measured pigment concentrations; and estimation using fluorescence measured by flow cytometry. Absorption by phytoplankton and nonphytoplankton particles was estimated using these methods for samples from four Biowatt cruises to the Sargasso Sea in March, May, August, and November 1987. Spectra obtained using these techniques will be compared and seasonal changes will be examined.

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58. Collins, D.J., D.A. Keifer, J.R. SooHoo, C. Stallings, and W.L. Yang, *A model for the use of satellite remote sensing for the measurement of primary production in the ocean*. in *Ocean Optics VIII*. 1986. Orlando, FL 637: p. 335-348. SPIE.

The estimation of oceanic primary production on a global scale is the focus of efforts in remote sensing using the Coastal Zone Color Scanner (CZCS). The goal of this research is to provide a measure of the primary production using only satellite data for the estimate. This estimate requires the measurement of surface pigments (chlorophyll *a* and phaeophytin *a*) using the CZCS, an estimate of the sea-surface temperature using the AVHRR and determination of the incident solar irradiance responses of phytoplankton to differing light and nutrient fields. This model includes the effects on production of variations in surface pigment concentration, the mixed layer depth and the dependence on the incident solar irradiance. The model has been tested using *in situ* data provided by the Southern California Bight Studies (Eppley, *et al.*, 1979) California Cooperative Fisheries Investigations (CalCOFI), Organization of Persistent Upwelling Structures (J.B. SooHoo in OPUS Data Report) and other data sets. A synoptic measure of the distribution of surface pigments is derived from the West Coast Chlorophyll and Temperature Time Series (West Coast Time Series Advisory Group, 1985). The features and behavior of the model will be presented together with the results of the model verification.

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59. Cullen, J.J., C.M. Yentsch, T.L. Cucci, H.L. MacIntyre, *Autofluorescence and other optical properties as tools in biological oceanography*. in *Ocean Optics IX*. 1988. Orlando, FL 925: p. 149-156. SPIE.

Bulk fluorescence measurements have been popular in algal culture studies and in oceanographic and limnological applications. Usually, fluorescence is interpreted as an indicator of chlorophyll concentration or phytoplankton biomass, but sometimes measurements of fluorescence can be related to physiological properties of phytoplankton, such as responses to light. Now that *in situ* fluorometers are being deployed routinely with optical packages, there is active interest in interpreting the relationships between fluorescence, beam transmission, diffuse attenuation, and the physiological characteristics of phytoplankton. Flow cytometry offers the potential to extend these interpretations to the scale of individual cells. It may be difficult to compare measurements of fluorescence, however, because instruments differ greatly in excitation irradiance and time scale of measurement.

With this in mind, we examined the short-term responses of a marine diatom to bright light, comparing different instruments (Sea Tech *in situ* fluorometer, Turner Designs fluorometer, EPICS flow cytometer, FACS analyzer, SeaTech beam transmissometer) while making concurrent measurements of photosynthesis vs irradiance and absorption spectra. Each fluorometer yielded somewhat different information, yet all showed a similar pattern of inhibition after exposure. One instrument, the *in situ* pulsed fluorometer, could show rapid changes of fluorescence immediately after large shifts of irradiance. Beam attenuation did not decline with the bright light treatment, nor did the specific absorption of chlorophyll. Photosynthetic efficiency was reduced after exposure to bright light, but the capacity for photosynthesis in high irradiance increased at the same time. These results are preliminary: nonetheless they support some interpretations of fluorescence/beam attenuation ratios, clarify some aspects of photosynthetic response to bright light, and suggest that flow cytometry may be useful for assessing physiological heterogeneity in phytoplankton assemblages.

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60. Davis, P., D.A. Caron, P.W. Johnson, and J.M. Sieburth, *Phototrophic and apochlorotic components of picoplankton and nanoplankton in the North Atlantic: geographic, vertical, seasonal and diel distributions*. Mar. Ecol. (Prog. Ser.), 1985. **21**(January 10): p. 15-26.

Chloroplast-containing and apochlorotic cells of nanoplankton (2 to 20  $\mu\text{m}$ ), and chroococcoid cyanobacteria and total bacteria in the picoplankton (0.2 to 2.0  $\mu\text{m}$ ) were enumerated by epifluorescence microscopy from 39 estuarine and oceanic stations to assess numerical relations of apochlorotic nanoplankton with other components of the microbial plankton. Apparent relations between different plankton types were found over geographic separation as well as seasonal and diel cycles. Population densities of apochlorotic, heterotrophic nanoplankton ( $H_{\text{nano}}$ ) and chloroplast-containing phototrophic nanoplankton ( $P_{\text{nano}}$ ) were similar, ranging from  $10^4$  cells  $\text{ml}^{-1}$  in estuarine environments to  $10^2$  cells  $\text{ml}^{-1}$  at oceanic stations. All microbial populations in the euphotic zone showed exponential decreases in concentration with increasing bottom depth. Vertical profiles showed decreasing abundance of all microbial populations with depth. Studies in Narragansett Bay, Rhode Island, indicated that  $H_{\text{nano}}$ ,  $P_{\text{nano}}$  and total picoplankton ( $T_{\text{pico}}$ ) followed trends similar to each other over winter/spring and summer blooms.  $H_{\text{nano}}$  were positively correlated with  $T_{\text{pico}}$  populations one week earlier, suggesting a predator/prey relationship. Diel studies at oceanic stations and in mesocosms in Narragansett Bay revealed positive correlations between  $T_{\text{pico}}$  and  $H_{\text{nano}}$  populations which may represent small internal temporal changes. These data suggest an abundant and dynamic  $H_{\text{nano}}$  population in the marine plankton which reflects changes observed in other components of the microbial plankton.

SEAMOcean, Inc., P.O. Box 1627, Wheaton, Maryland 20902. (Sieburth has reprints: Graduate School of Oceanography, University of Oceanography, Kingston, Rhode Island)

61. Davis, R.F. and C.R. Booth, *Correlation between solar-induced fluorescence and primary production*, Eos, 1987. **68**: p. 1694.

The relationship between primary production and solar-induced fluorescence throughout the day was examined with a Biospherical Instruments multichannel spectroradiometer (MER-2020) moored in Case II waters off the dock of the University of Washington Labs, Friday Harbor, WA. Concurrently, water samples were taken periodically for measurements of chlorophyll *a* concentration, primary production by 30 minute *in situ*

incubations, and spectral photosynthesis vs. irradiance (P vs. I) Solar-induced *in vivo* fluorescence of chlorophyll *a* was measured as the upwelling radiance centered at 683 nm and was directly correlated with primary production. The P vs. I relationship, in conjunction with downwelling irradiance measurements, provided an alternate, independent estimate of primary production. Chlorophyll *a* concentration and downwelling irradiance were not linearly related to solar-induced fluorescence. This data set provides a test for physiologically-based models for predicting primary production from *in vivo* chlorophyll *a* fluorescence. School of Oceanography, University of Washington, Seattle, WA 98195

62. Demetriades-Shah, T.H., M.D. Steven, and J.A. Clark, *High resolution derivative spectra in remote sensing*. Remote Sens. Environ., 1990. 33: p. 55-61.

The use of derivative spectra is an established technique in analytical chemistry for the elimination of background signals and for resolving overlapping spectral features. Application of this technique for tackling analogous problems such as interference from soil background reflectance in the remote sensing of vegetation or for resolving complex spectra of several target species within individual pixels in remote sensing is proposed. Methods for generating derivatives of high spectral resolution data are reviewed. Results of experiments to test the use of derivatives for monitoring chlorosis in vegetation show that derivative spectral indices are superior to conventional broad-band spectral indices such as the near-infrared/red reflectance ratio. Conventional broad-band indices are sensitive to both leaf cover as well as leaf color. New derivative spectral indices which were able to monitor chlorosis unambiguously were identified. Potential areas for the application of this technique in remote sensing are considered.

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63. Eppley, R.W. *Relations between primary production and ocean chlorophyll determined by satellites*. in *Global Ocean Flux Study Workshop*. 1984. Woods Hole, MA.

One purpose of the Global Flux Experiment is to define the rate of production of organic matter (including biogenic opal and calcium carbonate) as a function of geographic location and time. Several years were required to develop a comprehensive geographic overview of primary production in the ocean using ships and the  $^{14}\text{C}$  method. This global data set is by no means synoptic. Seasonal and interannual variability is known for only a few regions. Differences in methodology have resulted in non-uniform measurements and interpretation. The synoptic, large-scale measurements of near-surface chlorophyll, made possible by the CZCS suggest it may be possible to achieve global coverage of ocean chlorophyll in the next decade using an Ocean Color Imager. The chlorophyll would then be related to phytoplankton biomass and global oceanic  $\text{CO}_2$  fixation. Measurements from buoys, ships and aircraft would be required to identify the biological and physical factors associated with the variances in chlorophyll and its relation to biomass and production. The synoptic assessments, allowed for the first time by satellite images, open a new range of possibilities for uses of ocean production data. In view of these prospects, colleagues with primary production data are urged to examine their own data sets from the perspective of satellite chlorophyll measurement. There is much to be done.

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64. Eppley, R.W., E. Stewart, M.R. Abbott, and R.W. Owen, *Estimating ocean production from satellite-derived chlorophyll - Insights from the EASTROPAC data set*. in *Symposium on Vertical Motion in the Equatorial Upper Ocean and Its Effects Upon Living Resources*. 1985, Paris.

The EASTROPAC expedition took place in 1967-68 in the eastern tropical Pacific Ocean. Primary production was related to near-surface chlorophyll in these data. Much of the variability in the relation was due to the light-history of the phytoplankton and its photo-adaptive state. This was due to changes in the depth of mixing of the surface waters more than to changes in insolation. Accurate estimates of production from satellite chlorophyll measurements may require knowledge of the temporal and spatial variation in mixing of this region.

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65. Eppley, R.W., E. Stewart, M.R. Abbott, and U. Heyman, *Estimating ocean primary production of satellite chlorophyll - Introduction to regional differences and statistics for the Southern California Bight*. J. of Plankton Res., 1985. 7(1): p. 57-70.

The prospect of estimating primary production from chlorophyll pigment concentrations near the ocean surface is appealing, now that chlorophyll concentrations can be extracted from satellite images. Earlier work has shown that a proportionality between chlorophyll concentration and primary productivity exists, but with a large variation in the proportionality factor  $F$ . A cursory overview of global data suggests that part of this variability is regional. For example,  $F$  for subtropical open ocean regions exceeds that of temperate coastal regions. In the richest waters,  $F$  approaches a minimum limit value of about  $100 \text{ mg C m}^{-2}\text{d}^{-1}$  for a  $\text{mg Chl } a \text{ m}^{-3}$ . Some variability in the relation over time and space in the Southern California Bight is related to environmental variables. In the simplest systems,  $F$  is proportional to insolation. The variability in  $F$  may be of ecological interest beyond its utility in relating water column production to near-surface chlorophyll as an additional descriptive characteristic of pelagic ecosystems.

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66. Esaias, W.E., *Remote sensing of oceanic phytoplankton: Present capabilities and future goals*. 1980. in Primary Productivity in the Sea, P.G. Falkowski, Editor. New York & London, Plenum Press: p. 321-338.

The purpose of this review paper is to describe in broad detail some current research in the areas of sensor development and problems in integration which are being addressed. This necessitates a discussion of relevant problems in phytoplankton ecology, spatial and temporal domains, and available platforms and sensor combinations to address them. Finally some near-term expectations and longer-term goals and perceived directions for remote sensing technology are presented.

NASA, Langley Research Center, Hampton, Virginia, 23665

67. Esaias, W.E., G.C. Feldman, C.R. McClain, and J.A. Elrod, *Monthly satellite-derived phytoplankton pigment distribution for the North Atlantic ocean basin*. Eos, 1986. 67(44): p. 835-837.

CZCS data were processed to level 2 (plant pigments and diffuse attenuation coefficients) only for 2% of the raw data. Now, progress made in data processing, the successful application of satellite-derived ocean color data, the need to examine large data volumes to identify and correct algorithm deficiencies, the need to rewrite tapes to preserve data, and the need for improved estimates of global-scale primary production have engendered a revision of CZCS data processing within the Nimbus Project at NASA. The major objective of this revised CZCS processing effort is to produce global composites of the prime geophysical properties. This effort will commence fall 1986.

Oceans and Ice Branch of NASA Goddard Space Flight Center, Greenbelt, MD 20771 (Esaias)

68. Everitt, D.A., S.W. Wright, J.K. Volkman, D.P. Thomas, and E.J. Lindstrom, *Phytoplankton community compositions in the western equatorial Pacific determined from chlorophyll and carotenoid pigment distributions*. Deep-Sea Research, 1990. 37(6): p. 975-997.

The chlorophyll and carotenoid pigment compositions of particulate matter from 11 locations in the western equatorial Pacific were analysed by high performance liquid chromatography (HPLC). Chlorophyll *a* (Chl *a*) concentrations were generally low, as is common in oligotrophic waters, but they differed by more than an order of magnitude between locations (0.01-0.34 µg/l). Chlorophyll *b* concentrations were high at most stations, and higher than Chl *a* at one site on the equator. Major carotenoids included zeaxanthin, 19'-hexanoyloxyfucoxanthin, and 19'-butanoyloxyfucoxanthin. Peridinin, prasinoxanthin and fucoxanthin were present in low concentrations at every station (0-16 ng/l), but alloxanthin was found at only three sites. The concentrations of marker pigments were used in conjunction with Chl *a*/pigment ratios characteristic of the different algal classes to derive the composition (by class) of the phytoplankton communities. These calculations suggest that the phytoplankton communities are dominated by algal classes which mainly contain nanoplanktonic species. Prymnesiophytes were abundant at most stations, whereas green algae, cyanobacteria and prochlorophytes were important in specific areas. Although diatoms are usually the major source of fucoxanthin in productive water bodies, in these equatorial waters, prymnesiophyte contributions were much more important. Diatoms were not abundant at any station. Community composition and biomass showed greater variation than has been reported for other oligotrophic regions, probably due to local features such as water mixing near the equator and off the coast of Papua New Guinea. Some of the advantages and limitations of HPLC analysis of marker pigments for the determination of phytoplankton community compositions in oceanic waters are discussed. Note: The use of pigments as algal markers depends on how specific the marker pigments are for the various algal groups. Some marker pigments are not present in all species within an algal class. Similarly, only peridinin-containing dinoflagellates can be recognized; heterotrophs, fucoxanthin-containing species or those having other pigments due to endosymbiotic chrysophytes or cyanobacteria are not detected by this method. Zeaxanthin and chlorophyll *b* seem to be derived from prochlorophytes, so it can no longer be assumed that zeaxanthin is derived mainly from cyanobacteria. CSIRO Division of Oceanography., GPO Box 1538. Hobart, Tasmania 7001, Australia

69. Falkowski, P.G. (editor) *Primary Productivity in the Sea*. 1983. New York and London, Plenum Press (531 pages). Vol. 31, Brookhaven Symposia in Biology.

Primary productivity in the sea accounts for approximately 30 percent of the total global annual production. Holistic understanding of the factors determining marine productivity requires detailed knowledge of algal physiology and of hydrodynamics. Traditionally studies of aquatic primary productivity have been conducted by workers in two major schools: experimental laboratory biology, and empirical field ecology. Here an attempt was made to bring together people from both schools to share information and concepts; each author was charged with reviewing his or her field of expertise. The scope of the Symposium is broad, which we feel is its strength. Particularly valuable chapters are those by Shirley W. Jeffrey on Algal Pigment Systems, and by Wayne Esaias on Remote Sensing of Oceanic Phytoplankton: Present Capabilities and Future Goals. Each is listed separately in this bibliography. Jeffrey's chapter includes a diagram of possible phylogenetic relationships among the algae, and *in vivo* absorption spectra of several members each in three algal divisions, brown, green, and the biliprotein-containing line. Other valuable figures are the structures and absorption spectra of the major light-harvesting carotenoids. Brookhaven National Laboratory, Upton, New York 11973.

70. Falkowski, P.G., I. Dubinsky, and K. Wyman, *Growth-irradiance relationships in phytoplankton*. Limnol. Oceanogr., 1985. 30(2): p. 311-321.

The steady state growth rates of three species of marine phytoplankton, *Thalassiosira weissflogii*, *Isochrysis galbana*, and *Prorocentrum micans*, were followed in turbidostat culture. At each growth irradiance, photosynthesis and respiration were measured by following changes in oxygen. Together with measurements of optical absorption cross sections, cellular chlorophyll, carbon and nitrogen, and excretion rates as well as knowledge of the quantum flux, the quantum requirement for growth and photosynthesis were calculated. Our results suggest that there are variations in growth rate as well as changes in optical absorption cross sections for a given species. Interspecific differences in growth rate at a given irradiance are not related to changes in respiration however, but are primarily attributable to differences in optical absorption cross sections normalized to chlorophyll *a* and differences in chlorophyll:carbon ratios.

Oceanographic Sciences Division, Brookhaven National Laboratory, Upton, NY 11973

71. Falkowski, P.G. and D.A. Kiefer, *Chlorophyll *a* fluorescence in phytoplankton: Relationship to photosynthesis and biomass*. J. Plankton Res., 1985. 7(5): p. 715-731.

The theoretical and applied aspects of *in vivo* chlorophyll fluorescence are reviewed for aquatic biologists who use fluorescence in estimating standing stocks and photosynthetic activity. The major advantage of using fluorescence is that the measurement is easy to make. However, despite some sound theoretical models describing variable fluorescence there are many environmental factors influencing fluorescence about which little is known. Much more basic research on fluorescence-photosynthesis relationships needs to be done before fluorescence *per se* can replace current <sup>14</sup>C or O<sub>2</sub> methods for measuring primary productivity.

Oceanographic Sciences Division, Brookhaven National Laboratory, Upton, NY 11973

72. Falkowski, P.G. *Measurements of biophysical parameters used to derive phytoplankton photosynthetic rates by pump and probe fluorometry*. Aquatic Sciences Meeting, Am. Soc. Limnol. Oceanog., 1992. Santa Fe, NM.

The photoreduction of inorganic carbon to organic material by phytoplankton can be calculated from knowledge of three parameters: Quantum yields, the absorption cross section of the photosynthetic apparatus, and the electron transport time from water (the reducing agent) to CO<sub>2</sub> (the principal compound being reduced). Using pump and probe fluorometry in a variety of oceanic regimes, we have begun to describe the climatology of the three parameters and compared fluorescence-derived production estimates with radiocarbon measurements. The variance in quantum yields and cross sections appears to be related to the availability of nutrients. In his oral presentation, Falkowski noted that the absorption cross section (which for blue light is 400 Å<sup>2</sup>/quantum) decreases with increased brightness, and increases with nutrient-deficient cells.

Brookhaven National Laboratory, Upton, NY 11973

73. Frazel, D.W. and G. Berberian, *Distributions of chlorophyll and primary productivity in relation to water column structure in the eastern North Atlantic Ocean*. Global Biogeochemical Cycles, 1990. 4(3): p. 241-251.

Latitudinal variations in the megascale (10<sup>3</sup> km) distribution of biological properties are described in relation to water column structure between 60° and 7° N in the eastern North Atlantic Ocean. Stations were occupied along a meridional transect of stations at 20° W in August-September 1988, during the third leg of the National Oceanic and Atmospheric

Administration Global Change Expedition. An additional transect to the south (38° N to 7° N) was occupied to extend the total range of latitudinal observations. Chlorophyll *a* concentrations were highest in the northern latitudes (<2.51 mg/m<sup>3</sup>) (*sic*), decreasing to >0.2 mg/m<sup>3</sup> (*sic*) in the vicinity of the subtropical gyre, south of 40° N. The nitracline was associated with a shoaling of the pycnocline in the northern latitudes. At 7° N, high chlorophyll concentrations (approximately 0.5 mg/m<sup>3</sup>) and enhanced primary productivity (375.5 mg C m<sup>-2</sup>d<sup>-1</sup>) were associated with a lens of fresh Amazon River water. Primary productivity rates were variable throughout the transect, ranging from 646 to 136 mg C m<sup>-2</sup>d<sup>-1</sup>. Productivity maxima were located south of Iceland, at 46° N and in the vicinity of the Azores Front at 35° N. Latitudinal distributions of primary productivity corresponded closely to a model of productivity along a transect at 40° N by Yentsch. Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, FL 33149-1098

74. Gallegos, C.L., D.L. Correll, and J.W. Pierce, *Modeling spectral diffuse attenuation, absorption, and scattering coefficients in a turbid estuary*. Limnol. Oceanogr., 1990. 35(7): p. 1486-1502.

Spectral diffuse attenuation coefficients were measured in the Rhode River and Chesapeake Bay, Maryland, on 28 occasions in 1988 and 1989. The model of Kirk was used to extract scattering and absorption coefficients from the measurements in waters considerably more turbid than those in which the model was previously applied. Estimated scattering coefficients were linearly related to mineral suspended solids. Estimates of total absorption coefficients were decomposed as the sum of contributions by water, dissolved organic matter, phytoplankton chlorophyll, and particulate detritus, each having a characteristic spectral shape. The 1988 data were used to develop a model of scattering and absorption coefficients based on the specific curves regressed against water-quality parameters. Diffuse attenuation coefficients in the 1989 data ranging from 1 to 10 m<sup>-1</sup> and photic depths ranging from <1 to 4.5 m were predicted with a C.V. of about 25%. The problem of estimating concentrations of water-quality constituents from optical measurements was indeterminate due to the similarity in shape of the specific curves of dissolved substances and depigmented particulates. Chlorophyll concentration could be estimated because it was strongly related to water-corrected absorption in the 670 nm waveband, but several outliers occurred due to biological variability in specific absorption of pigments. Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037

75. Glover, H.E., B.B. Prezelin, L. Campbell, and M. Wyman, *Pico- and ultra-plankton Sargasso Sea communities: Variability and comparative distributions of Synechococcus species and algae*. Mar. Ecol. (Prog. Ser), 1988. 49(1-2): p. 127-139.

Ultraplankton (0.2 to 5 µm) provided >88% of euphotic layer chlorophyll (Chl) at 2 Sargasso Sea stations in July/August 1986. Communities were further characterized to quantify the separate abundances of phycoerythrin-fluorescing cyanobacteria *Synechococcus* spp. and Chl-fluorescing algae in 0.2 to 0.6, 0.6 to 1 and 1 to 5 µm size fractions. Throughout the water-column at both stations, the majority of *Synechococcus* cells were consistently found in the 0.6 to 1 µm fraction; the Sargasso Sea WH7803 serogroup was not a dominant component of *Synechococcus* populations at any depth. Highest numbers of *Synechococcus* cells were always in the surface isothermal layer, where they accounted for > 95% of all ultraphytoplankton cells. At the base of the euphotic layer total numbers of photoautotrophs were low, but numbers of algae increased. The varying distribution of the 2 ultraphytoplankton components with depth was reflected in their separate contributions to Chl concentrations, and algae were the main contributors to Chl maxima at 1 to 3% I<sub>0</sub>. Above



this depth, a pigment maximum in phycoerythrin (PE) occurred at the nitracline, coincident with a peak in primary productivity. PE maxima were due to an increase in PE content of *Synechococcus cells* and not to an increase in their abundance. The 2 stations did however exhibit significant differences. High surface productivity at Station 1 was supported by nanomolar changes in nitrate concentrations, which selectively and rapidly induced a *Synechococcus* bloom. In contrast, the water-column characteristics of Station 2 were relatively stable; *Synechococcus* spp. were less abundant throughout the water column, while algae were twice as abundant at the Chl maximum and 0.5% light level where most were of picoplankton size (79 to 89 % of algae were in <1µm fractions). Data suggest that there is a considerable degree of variability in the abundance, composition, and productivity of stratified oceanic ultraphytoplankton communities.

Bigelow Laboratory for Ocean Sciences, W. Boothbay Harbor, ME 04575

76. Glover, H.E., B.B. Prezelin, L. Campbell, M. Wyman, and C. Garside, *Observations of a nitrate-dependent Synechococcus bloom in surface Sargasso Sea water*. Nature, 1988. 331(6152): p. 161-163.

Considerable debate exists concerning the magnitude of oceanic primary production, its rate of transfer to other trophic levels and turnover times of carbon and nitrogen. In nitrogen-limited ocean systems, episodic increases in nitrate concentrations can support a significant fraction of annual phytoplankton production. Yet little information is available regarding the distribution of nitrate in seasonally stratified oceanic surface waters because concentrations are below the 0.03 µM detection limit of colorimetric methods. We present the first evidence that high surface productivity in stratified Sargasso Sea water was supported by nanomolar changes in nitrate concentrations. This change was stoichiometrically consistent with the subsequent cellular production of a cyanobacterial (*Synechococcus*) bloom. Initially, cellular phycoerythrin and chlorophyll pigments increased, after which growth was enhanced to near maximum rates, and grazing was closely coupled to production. These observations suggest that *Synechococcus* occupies an important trophic position in the transfer of new nitrogen into the ocean food web.

Bigelow Lab for Ocean Sci., McKown Point, West Boothbay Harbor, ME 04575

77. Goodwin, T.W., *The Biochemistry of Carotenoids*. 1980, London: Chapman & Hall. This text is an essential reference, especially the chapter on algae (Chap. 7) It covers the structures, occurrence, functions and uses of carotenoids.

78. Gordon, H.R., *Diffuse reflectance of the ocean: the theory of its augmentation by chlorophyll a fluorescence at 685 nm*. Applied Optics, 1979. 18: p. 1161-1166.

The radiative transfer equation is modified to include the effect of fluorescent substances and solved in the quasi-single scattering approximation for a homogeneous ocean containing fluorescent particles with wavelength-independent quantum efficiency and a Gaussian-shaped emission line. The results are applied to the *in vivo* fluorescence of chlorophyll *a* in phytoplankton in the ocean to determine if the observed quantum efficiencies are large enough to explain the enhancement of the ocean's diffuse reflectance near 685 nm in chlorophyll-rich waters without resorting to anomalous dispersion. The computations indicate that the required efficiencies are sufficiently low to account completely for the enhanced reflectance. The validity of the theory is further demonstrated by deriving values for the upwelling irradiance attenuation coefficient at 685 nm which are in close agreement with the observations.

National Oceanic and Atmospheric Administration, Environmental Research Laboratories, Pacific Marine Environmental Laboratory, Seattle, WA 98105

79. Gordon, H.R., J.L. Mueller, and R.C. Wrigley, *Atmospheric correction of Nimbus-7 Coastal Zone Color Scanner Imagery*, in *Remote Sensing of Atmospheres and Oceans*, E. Deepak, Editor. 1980, Academic Press: New York. p. 457-483.

The Coastal Zone Color Scanner (CZCS) on NIMBUS-7 is a scanning radiometer designed to view the ocean in six spectral bands (centered at 443, 520, 550, 670, 750, and 11,500 nm) for the purpose of estimating sea surface chlorophyll and temperature distributions. In the visible bands, the atmosphere obscures the imagery to the extent that at 443 nm, at most, only 20 percent of the observed radiance originates from beneath the sea surface. Retrieving this subsurface radiance from the imagery is complicated by the highly variable nature of the aerosol's contribution. In this paper, an algorithm for the removal of these atmospheric effects from CZCS imagery is described, a preliminary application of the algorithm to an image with very strong horizontal variations in the aerosol optical thickness is presented, and retrieval of the spatial distribution of the aerosol optical thickness is discussed.

Dept. of Physics, University of Miami, Coral Gables, FL 33124

80. Gordon, H.R., D.K. Clark, J.W. Brown, O.B. Brown, R.H. Evans, and W.W. Broenkow, *Phytoplankton pigment concentrations in the Middle Atlantic Bight: Comparison between ship determinations and Coastal Zone Color Scanner estimations*. *Applied Optics*, 1983. 22: p. 20-36.

The processing algorithms used for relating the apparent color of the ocean observed with the Coastal Zone Color Scanner on Nimbus-7 to the concentration of phytoplankton pigments (principally the pigment responsible for photosynthesis, chlorophyll *a*) are developed and discussed in detail. These algorithms are applied to the shelf and slope waters of the Middle Atlantic Bight and also to Sargasso Sea waters. In all, four images are examined, and the resulting pigment concentrations are compared to continuous measurements made along ship tracks. The results suggest that over the 0.08-1.5 mg/m<sup>3</sup> range the error in the retrieved pigment concentration is of the order of 30-40% for a variety of atmospheric turbidities. In three direct comparisons between ship-measured and satellite-retrieved values of the water-leaving radiance the atmospheric correction algorithm retrieved the water-leaving radiance with an average error of ~10%. This atmospheric correction algorithm does not require any surface measurements for its application.

Dept of Physics, University of Miami, Coral Gables, FL 33124.

81. Gordon, H.R., O.B. Brown, R. H. Evans, J.W. Brown, R.C. Smith, K.S. Baker, and D.K. Clark, *A semianalytic radiance model of ocean color*. *J. of Geophys. Res.*, 1988. 93(D9): p. 10909-10924.

A semianalytic radiance model is developed which predicts the upwelled spectral radiance at the sea surface as a function of the phytoplankton pigment concentration for Morel Case 1 waters. The model is in good agreement with experimental measurements carried out in waters which were not included in the data base used to derive it. It suggests that the observed variability in the radiance is due to variations in the backscattering of plankton and the associated detrital material. The model is extended to include other material in the water, such as dissolved organic material, referred to as yellow substances, and detached coccoliths from coccolithophorids, e.g. *Emiliana huxleyi*. Potential applications include an improved bio-optical algorithm for the retrieval of pigment concentrations from satellite imagery in the presence of interference from detached coccoliths and an improved atmospheric correction for satellite imagery. The model also serves to identify and to interpret deviations from Case 1 waters. (Case 1 waters are those in which the optical properties of the water are controlled by phytoplankton and their immediate detritus.)

Dept. of Physics, University of Miami, Coral Gables, FL 33124

82. Gowen, R.J., P. Tett, and B.J.B. Wood, *Changes in the major dihydroporphyrin plankton pigments during the spring bloom of phytoplankton in two Scottish Sea-Lochs*. J. Mar. Biol. Ass. U.K., 1983. 63: p. 27-36.

A chromatographic/fluorometric method was used to measure changes in the proportions of four planktonic dihydroporphyrin pigments during the spring bloom of 1979 in two fjordic sea-lochs, Creran and Etive, on the west coast of Scotland. Very little pheophytin *a* was detected during the bloom. Chlorophyll *a*, and to a lesser extent chlorophyllide *a*, were the two main pigments found during the bloom. During senescence the main pigment breakdown route appeared to be via chlorophyllide *a* to pheophorbide *a*. These results suggest that standard methods for measurement of 'chlorophyll' which do not distinguish between chlorophyll *a* and chlorophyllide *a* might significantly over-estimate the photosynthetic potential of phytoplankton.  
Scottish Marine Biological Association, Dunstaffnage Marine Research Laboratory,  
P.O. Box 3, Oban, Argyll, PA34 4AD, Scotland

83. Gower, J.F.R. and G. Borstad, *Use of the in vivo fluorescence line at 685 nm for remote sensing surveys of surface chlorophyll *a**, in *Oceanography from Space*, J.F.R. Gower, Editor. 1981, Plenum: New York. p. 329-338.

In airborne surveys of coastal water the *in vivo* fluorescence line of chlorophyll *a* provides a characteristic and relatively narrow band signature for chlorophyll detection and measurement. Quantitative accuracy is limited by the varying fluorescent efficiency of different phytoplankton populations and by changes in water absorption that reduce the light available for fluorescence, but this accuracy appears adequate for many survey applications. Examples are shown of airborne measurements taken as part of the Canada France Ocean Optics Experiment (CFOX) over the Mediterranean, the coastal waters of British Columbia and the Lancaster Sound area of the eastern Canadian arctic. The fluorescence observations appear to give as useful a signal as the blue to green reflectance ratio with less uncertainty due to atmospheric scattering and surface reflection. From higher altitudes the effects of oxygen and water vapour absorption lines become important, but the line remains measurable, and mapping of the fluorescence distribution from space appears feasible.  
Institute of Ocean Sciences, 9860 West Saanich Road, P.O. Box 6000, Sidney,  
B.C. V8L 4B2 Canada

84. Guillard, R.R.L., L.S. Murphy, P. Foss, and S. Liaaen-Jensen, *Synechococcus spp. as likely zeaxanthin-dominant ultraphytoplankton in the North Atlantic*. Limnol. Oceanogr., 1985. 30(2): p. 412-414.

We present four lines of evidence consistent with the suggestion of Gieskes and Kraay that the  $<1\ \mu\text{m}$  particles observed in North Atlantic seawater associated with the carotenoid zeaxanthin are cyanobacteria (*Synechococcus* spp). First, four quite different clones of marine *Synechococcus* contain zeaxanthin as their main carotenoid (50-80% of total carotenoids). Second, none of the other ultraplankters we have yet studied contains more than traces of zeaxanthin, though they contain other pigments potentially useful as chemo-systematic markers. Third, none of the other "diagnostic" carotenoids was reported by Gieskes and Kraay. Fourth, the latitudinal gradient of zeaxanthin reported correlates well with our observations of the abundance of *Synechococcus* but not of other ultraplankters in the North Atlantic. The circumstantial evidence is strong and merits direct confirmation.  
Bigelow Laboratory for Ocean Sciences, McKown Point, West Boothbay Harbor,  
Maine 04575 and Organic Chemistry Laboratories, Norwegian Institute of Technology,  
University of Trondheim, N-7034 Trondheim, Norway

85. Hallegraeff, G.M., *Seasonal study of phytoplankton pigments and species at a coastal station off Sydney: Importance of diatoms and the nanoplankton*. Mar. Biol., 1981. 61: p. 107-118.

Phytoplankton pigments and species were studied at a coastal station off Sydney (New South Wales, Australia) over one annual cycle. Sudden increases in chlorophyll *a* (up to 280 mg m<sup>-2</sup>), due to short-lived diatom blooms, were found in May, July, September, January and February. These were superimposed upon background levels of chlorophyll *a* (20-50 mg m<sup>-2</sup>), due mostly to nanoplankton flagellates, which occurred throughout the year. The nanoplankton (<15 µm) accounted for 50 to 80% of the total phytoplankton chlorophyll. The annual cycle of populations of 16 dominant species-groups was followed. Possible explanations as to alternation of diatom-dominated and nanoplankton-dominated floras are discussed. Thin-layer chromatography of phytoplankton pigments was used to determine the distribution of algal types, grazing activity, and phytoplankton senescence in the water column. Chlorophyll *c* and fucoxanthin (diatoms and coccolithophorids) and chlorophyll *b* (green flagellates) were the major accessory pigments throughout the year, with peridinin (photosynthetic dinoflagellates) being less important. Grazing activity by salps and copepods was apparent from the abundance of the chlorophyll degradation products pheophytin *a* (20 to 45% of the total chlorophyll *a* and pheophorbide *a* (10 to 30%). Chlorophyllide *a* (20 to 45%) was associated with blooms of *Skeletonema costatum* and *Chaetoceros* spp. Small amounts of other unidentified chlorophyll *a* derivatives (5 to 20%) were frequently observed. (Main groups are: chain-forming diatoms, dinoflagellates, prymnesiophytes, prasinophytes, cryptomonads)  
CSIRO Division of Fisheries and Oceanography; P.O. Box 21, Cronulla, New South Wales 2230 Australia

86. Hamilton, M.K., C.O. Davis, S.H. Pilorz, W.J. Rhea, and K.L. Carder, *Examination of chlorophyll distribution in Lake Tahoe, using the Airborne Visible/Infrared Imaging Spectrometer (AVIRIS)*. in *Third Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) Workshop*. 1991. Pasadena, California: Jet Propulsion Laboratory: p. 289-301.

An AVIRIS image was obtained for Lake Tahoe, California, on August 9, 1990, along with *in situ* data. Profiles of percent transmission of light, stimulated chlorophyll fluorescence, photosynthetically available radiation, and upwelling and downwelling irradiance and upwelling radiance in several spectral bands were measured in the water column, as well as the above-water spectral distribution of light. The image was atmospherically corrected using the LOWTRAN 7 atmospheric model, and the resulting image was examined for the presence of spurious periodicities. The low concentration of chlorophyll in the lake provided an increase in the radiance in the chlorophyll absorbing band, to the extent that pigment concentrations could be accurately modeled using a variant of the CZCS algorithm with the AVIRIS image. Although limnological sampling of the lake was insufficient for good statistical results, AVIRIS now appears to be useful in the mapping of surface chlorophyll in low concentrations, as are found in the oligotrophic ocean.  
Jet Propulsion Laboratory, California Institute of Technology, Pasadena, California

87. Hayward, T.L. and E.L. Venrick, *Relation between surface chlorophyll, integrated chlorophyll and integrated primary production*. Marine Biology, 1982. 69: p. 247-252.

The relationship between surface chlorophyll and integrated values of chlorophyll and primary production are examined in the California Current and the central North Pacific Ocean. In the California Current, surface chlorophyll is correlated with both integrated chlorophyll and integrated primary production, although there is considerable scatter in the relationships. In the central North Pacific, surface chlorophyll is not correlated with either

integrated chlorophyll or integrated primary production. An analysis of closely spaced replicate casts shows that in both areas most of the scatter in the relations between surface values and integrated values is due to spatial or temporal changes in the relations themselves rather than measurement error. The use of surface chlorophyll or fluorescence values as indicators of the biological state of pelagic ecosystems should thus be applied with caution.

Marine Life Research Group, Scripps Institution of Oceanography, A-028, La Jolla, California 92093

88. Hoge, F.E. and R.N. Swift, *Airborne dual laser excitation and mapping of phytoplankton photopigments in a Gulf Stream Warm Core Ring*. Applied Optics, 1983. 22: p. 2272-2280.

Utilization of a two-color airborne lidar system in the systematic study of a major oceanographic feature is reported here for the first time. An excimer pumped dye laser was optically and electronically integrated into the NASA Airborne Oceanographic Lidar for simultaneous use with a frequency doubled Nd:YAG laser. The output beams exit the laser system along parallel paths after being produced on an alternating pulse basis at a combined rate of 12.5 pps. Results are presented for missions flown over a Gulf Stream Warm Core Ring (WCR) as well as over shelf, slope, Gulf Stream, and Sargasso Sea waters. From the airborne data a high coherence is shown between the two-color chlorophyll *a* data and between the Nd:YAG chlorophyll *a* and phycoerythrin responses within each of these water masses. However, distinct differences in the response patterns of these photopigments are shown to exist between the different water masses. At certain of the boundaries separating the water masses a sharp transition is seen to occur, while at others a wider transition zone was observed in which the correlation between the photopigments appears to degrade. The conclusion is that the feasibility of acquiring fluorescence emission of phytoplankton photopigments using dual laser excitation has been demonstrated over different offshore water masses using an airborne fluorosensing system. Variations in the level of phycoerythrin relative to chlorophyll *a* represent differences in the planktonic assemblages comprising various water masses.

NASA Goddard Space Flight Center, Wallops Flight Facility, Wallops Island, Virginia 23337.

89. Holligan, P., M. Voillier, D.S. Harbour, P. Camus, and M. Champagne-Phillippe, *Satellite and ship studies of coccolithophore production along a continental shelf edge*. Nature, 1983. 304(28 July): p. 339-342.

Each year since the Coastal Zone Color Scanner (CZCS) was launched on the Nimbus 7 satellite, extensive patches of water giving strong reflectance of visible light have been observed during the early summer along the outer margin of the north-west European continental shelf between 45° and 60° N. Various hypotheses including coccolithophores, phytoplankton with external calcified plates or coccoliths, were suggested to explain a comparable feature on Landsat images for July 1977. To test these, we report here observations made from French and UK research vessels in 1982, using unprocessed CZCS images supplied by the University of Dundee and Centre de Meteorology Spatiale in Lannion to locate suitable sampling areas immediately before and during the cruise, and atmospherically corrected data from the European Space Agency for subsequent analysis and calibration of the reflectance signals. The high reflectance was found to be caused by a surface bloom of the widespread coccolithophore, *Emiliana huxleyi*, which also produced abundant detached coccoliths. This finding is of relevance to recent work both on the ecology of coccolithophores, including their importance in the sedimentation of biogenic carbon and lipids and in

palaeoclimatic studies, and on the development of reliable remote sensing techniques for the estimation of chlorophyll in oceanic waters.

Marine Biological Association, Citadel Hill, Plymouth PL1 2PB, UK

90. Holligan, P.M., M. Voillier, C. Dupouy, and J. Aiken, *Satellite studies on the distribution of chlorophyll and dinoflagellate blooms in the western English Channel*. Continental Shelf Res., 1983. 2: p. 81-96.

Surface phytoplankton populations, that persist for several weeks and over spatial scales >100km, can be monitored most effectively by satellite. We show how the Coastal Zone Color Scanner provides new information about the dynamics of dinoflagellate blooms, and discuss some problems with the application of the instrument. The estimated overall accuracy for measuring total chlorophyll, C (chlorophyll + phaeopigment), by satellite was  $\log C \pm 0.26$ . Maximum chlorophyll >30 mg/m<sup>3</sup> along the ferry route between Plymouth and Roscoff, and as high as 50 to 70 mg/m<sup>3</sup> to the northwest of Roscoff. *G. aureolum* form >95% of phytoplankton biomass between 23 July and 2 August, 1981.

Marine Biological Association of the U.S., Plymouth PL1 2PB, U.K.

91. Hooker, S.B., W.E. Esaias, G.C. Feldman, W.W. Gregg, C.R. McClain, *An Overview of SeaWiFS and Ocean Color*, NASA Technical Memorandum 104566, Vol. 1, 1992. SeaWiFS Technical Report Series. S.B. Hooker, ed. E.R. Firestone, Technical Ed. National Aeronautics and Space Administration, Goddard Space Flight Center, Greenbelt, Maryland 20771

SeaWiFS, the Sea-Viewing Wide Field-of-View Sensor, will bring to the ocean community a welcomed and improved renewal of the ocean color remote sensing capability lost when the Nimbus-7 Coastal Zone Color Scanner (CZCS) ceased operating in 1986. The goal of SeaWiFS, scheduled to be launched in August 1993, is to examine oceanic factors that affect global change. Because of the role of phytoplankton in the global carbon cycle, data obtained from SeaWiFS will be used to assess the ocean's role in the global carbon cycle, as well as other biogeochemical cycles. SeaWiFS data will be used to help elucidate the magnitude and variability of the annual cycle of primary production by marine phytoplankton and to determine the distribution and timing of spring blooms. The observations will help to visualize the dynamics of ocean and coastal currents, the physics of mixing, and the relationships between ocean physics and large-scale patterns of productivity. The data will help fill the gap in ocean biological observations between those of the CZCS and the Moderate Resolution Imaging Spectrometer (MODIS) on the Earth Observing Satellite-A (EOS-A).

Goddard Space Flight Center, Greenbelt, MD 20771

92. Hooks, C.E., R.R. Bidigare, M.D. Keller, and R.R.L. Guillard, *Coccoid eukaryote marine ultraplankters with four different HPLC pigment signatures*. J. Phycol., 1988. 24(4): p. 571-580.

Pigment compositions of 16 coccoid eukaryotic ultraplanktonic clones isolated from coastal and oceanic waters were investigated by high-performance liquid chromatography (HPLC). Four distinct pigment signatures were observed, and clones were classified into subgroups based on the presence or absence and relative abundances of selected chlorophylls and carotenoids. The first subgroup (5 clones) was pigmented like chlorophyll *b*-containing higher plants and resembled true chlorophyte algae. The second subgroup (3 clones) contained chlorophyll *b* and relatively high levels of prasinoxanthin, a carotenoid characteristic of certain members of the Prasinophyceae (sometimes grouped as the Micromonadophyceae). The third subgroup (5 clones) was pigmented in a similar fashion but had a twofold lower prasinoxanthin-to-chlorophyll *a* ratio and an unidentified carotenoid. The fourth

subgroup (3 clones) lacked chlorophyll *b* and was pigmented like certain members of the Chrysophyceae (e.g. 19'-butanoyloxyfucoxanthin-containing *Pelagococcus subviridis* Norris). On-line diode array spectral analysis of selected clonal extracts revealed the presence of Mg 2,4-divinylphaeoporphyrin *a*, monomethyl ester-like and chlorophyll *c*-like pigments in representatives of the prasinophyte-like and chrysophyte-like clones, respectively. These findings plus the occurrence of chlorophyll *b*, prasinoxanthin and 19'-butanoyloxyfucoxanthin in the North Atlantic Ocean suggest that chrysophyte- and prasinophyte-like organisms can be important biomass components of marine phytoplankton.

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93. Hord, R.M., *Remote Sensing - Methods and Applications*. 1986, New York: John Wiley & Sons. 362 p.

Digital image processing of remotely sensed data has grown into a mature discipline. A vigorous international research and development effort to enhance and extend our capabilities with these tools for numerically manipulating pictures continues to attract many of the technical community's best talents. However, a review of the current literature reveals a deficiency that this book attempts to redress by publishing a survey of practical topics. Thus, this is a collection of pragmatic information. This book is addressed to the experienced worker in the field of digital image processing of remotely sensed data. The volume is structured into three broad subjects: sensors, processing and analysis techniques, and applications. (Note: CZCS performance parameters and spectral response curves appear here.)

94. Hovis, W., E.F. Szajna, and W.A. Bohan, *Nimbus-7 CZCS Coastal Zone Color Scanner Imagery for Selected Coastal Regions*. 1988, NASA Goddard Space Flight Center.

Global observations from earth-orbiting satellites present an opportunity to study the vast areas of the oceans in a manner and timeframe impossible with ships or aircraft, since an area of 250,000 square miles can be observed in one minute. Ship and aircraft ocean color measurements showed that ocean color can be related to water content in a meaningful way, and the effects of interference by atmospheric backscatter of sunlight can be overcome. This atlas is intended to provide interpretations of CZCS products from the viewpoints of a wide range of oceanographic scientists as an introduction for those not already familiar with the potential of space for such information gathering. Images are presented from the Gulf of Alaska/Aleutian Islands/Bering Sea, the Pacific North American Coast, the Atlantic North American Coast, the Gulf of Mexico/Caribbean Sea, Western European Basin, Atlantic South American Coast, South Africa, and Antarctica.

95. Hunt, A.J., M.S. Quinby-Hunt, and D.B. Shapiro. *Effects of lambda-dependent absorption on the polarization of light scattered from marine Chlorella*. in *Ocean Optics X*. 1990. Orlando, FL 1302: p. 269-280. SPIE.

This paper investigates the wavelength dependence of the polarization characteristics of light scattered from laboratory cultures of marine *Chlorella*. Scattering measurements were obtained using a scanning polarization-modulation nephelometer at wavelengths of 457 and 514 nm. The experimental data are corrected for non-spherical contributions and the resulting curves compared to Mie calculations of coated spheres with a Gaussian size distribution. Although the absorption of *Chlorella* has been reported to be strongly wavelength-dependent in the blue to green region of the spectrum, the scattering behavior changes very little. To verify the sensitivity of the scattering technique to changes in the imaginary refractive index, measurements were performed on absorbing and non-absorbing suspensions of well-characterized, coated copolymer particles. In all cases, the

angle-dependent measurements and calculations were compared for four elements of the 16 element Mueller scattering matrix at two wavelengths. In the past, comparison of scattering models and measurements were generally performed for only the total intensity (one element of the scattering matrix). The use of four elements provides a much more stringent test of scattering calculations than those based on a single element. Using this method, we are able to infer information about the internal structure and refractive indices of microscopic single cell organisms *in vivo*.

Applied Science Division, Lawrence Berkeley Laboratory, University of California, Berkeley, CA 94720

96. Hurley, J.P. and D.E. Armstrong, *Fluxes and transformations of aquatic pigments in Lake Mendota, Wisconsin*. Limnol.Oceanogr., 1990. 35(2): p. 384-398.

Concentrations and fluxes of chlorophyll and carotenoid pigments were measured in suspended and settling particulate matter and in surface sediments in Lake Mendota. Flux comparisons were used to calculate the extent of alteration or degradation within the water column and at the sediment surface. Losses within the water column for specific time intervals ranged from almost negligible for diatoxanthin to 96% for peridinin. The extent of loss was influenced by pigment type and transport process.

Center for Limnology, University of Wisconsin, Madison, WI 53706.

97. Hurley, J.P. and C.J. Watras, *Identification of bacteriophylls in lakes via reverse-phase HPLC*. Limnol. Oceanogr., 1991. 36(2): p. 307-315.

Reverse-phase HPLC has been used successfully to quantify phytoplankton pigments in lakes and oceans. Here we extend the technique to photosynthetic bacterioplankton and demonstrate the identification of five bacteriochlorophylls extracted from pure cultures with 90% acetone. The technique was then applied to natural plankton samples from two oligotrophic lakes in northern Wisconsin. In both lakes, previously undetected layers of phototrophic bacteria were identified based on their pigment compositions. In one of the lakes, the bacterial layer previously had been misidentified as a deep zone of abundant pheopigment. These observations re-emphasize concerns that traditional protocols (i.e. measuring the absorbance of mixed acetone extracts at 665 nm before and after acidification) have serious limitations in natural systems and can lead to misinterpretations of planktonic distributions and processes. The potential importance of phototrophic bacteria in dimictic temperate lakes is demonstrated. Without significantly modifying standard reverse-phase HPLC protocols, unambiguous determinations of eucaryotic and procaryotic chlorophylls and degradation products can be made simultaneously.

Wisconsin Dept. of Natural Resources, Bureau of Research, 3911 Fish Hatchery Rd., Fitchburg WI 53711.

98. Hurley, J.P. and P.J. Garrison. *Identification of deep plankton in lakes by HPLC pigment analyses*. in Aquatic Sciences Meeting, Am. Soc. Limnol. Oceanog., 1992. Santa Fe, NM.

Deep planktonic production is a common feature of many deep, stratified lakes. Traditional protocols for chlorophyll analyses (fluorometry, spectrophotometry) enable detection of the presence of deep production, yet identification of composition usually requires microscopy. High Performance Liquid Chromatography (HPLC) offers the ability to rapidly identify major planktonic groupings by signature pigment (chlorophyll, carotenoid) analysis. We have applied this technique to five stratified lakes in Wisconsin and have noted many differences in deep planktonic composition among lakes. In mesotrophic Mirror and Shadow Lakes, deep maxima of myxoxanthophyll, oscillaxanthin, echinenone and zeaxanthin (blue-green algae) overlay bacteriochlorophylls (Bchl) *a*, *d*, and *e*. In oligotrophic Little Rock and



Russet Lakes, deep alloxanthin (cryptophytes) peaks overlay Bchl *d*. In contrast, oligotrophic Pallette Lake, deep fucoxanthin (chrysophytes) lutein (green algae) and alloxanthin overlay Bchl *e*. Typical carotenoid levels range from 0.2-10 µg/L and in some lakes (Mirror, Shadow, Little Rock) typical late summer Bchl levels exceed 100 µg/L. Bureau of Research, Wisconsin Department of Natural Resources. 3911 Fish Hatchery Road, Fitchburg, WI 53711

99. Jeffrey, S.W. *Algal Pigment Systems* in Primary Productivity in the Sea, 1980 P. G. Falkowsky, Editor. New York & London, Plenum Press: p. 33-58.

One-third of the earth's crust is occupied by land, and this supports a terrestrial vegetation receiving the full visible range of the sun's radiation. The other two-thirds of the earth's surface is occupied by the world's oceans, and these heavily filter the incident radiation. Even at a few meters' depth, the absorbing and scattering properties of water profoundly alter the light spectrum and reduce the intensity compared to that at the sea's surface. As a consequence, aquatic plants have evolved a variety of light-harvesting pigment systems for trapping those portions of the visible spectrum available. In contrast, only one light-harvesting pigment system has become dominant in terrestrial plants. The total algal flora, both macroscopic and microscopic forms, includes at least 2,100 genera and more than 27,000 species. Benthic algae are frequently found well below the 1% light level. To survive successfully in these light-limited marine habitats, the algae must be adapted to utilizing particular wavelengths of the full visible spectrum, usually at light intensities much reduced from those at the sea's surface. Jeffrey's chapter includes a diagram of possible phylogenetic relationships among the algae, and a table of the major light-harvesting pigments in algae. Figures include *in vivo* absorption spectra of several members each in three algal divisions, brown, green, and the biliprotein-containing line, as well as absorption and fluorescence emission spectra of chlorophylls *c1* and *c2*, and absorption spectra of the cyanobacterial biliproteins. Other valuable figures are the structures and absorption spectra of the major light-harvesting carotenoids.

CSIRO, Division of Fisheries and Oceanography, Cronulla, N.S.W. Australia

100. Jeffrey, S.W., M. Sielickie, and F.T. Haxo, *Chloroplast pigment patterns in dinoflagellates*. J. Phycol., 1975. 11: p. 374-384.

The chlorophylls and carotenoids of 22 species of dinoflagellates were analyzed by thin layer chromatography, using 2-dimensional sucrose plates, and 1-dimensional polyethylene plates for chlorophylls *c1* and *c2*. Peridinin was the major carotenoid in 19 of the species, while fucoxanthin was the major carotenoid in 3. In the peridinin-containing species, 5 carotenoid fractions, constituting more than 95% of the total carotenoids, were always present. These were peridinin (+/- neo-peridinin), averaging 64% of the total carotenoid, diadinoxanthin, dinoxanthin, b-carotene and a polar, unidentified pink xanthophyll. Six other carotenoid fractions occurred in minor or trace quantities among the species, but were not identified. Two of these had a wide distribution; the other 4 were restricted to one or 2 species. The chlorophyll content of the dinoflagellate cultures ranged from 1-141 µg chlorophyll *a* + *c*/10<sup>6</sup> cells, a pattern which was broadly correlated with cell size. In the peridinin-containing species the ratio of chlorophyll *a* to *c* on a molar basis was approximately 2 (range 1.60-4.39); in the fucoxanthin-containing species this ratio was approximately 4 (range 2.65-5.73). Both chlorophylls *c1* and *c2* occurred in the fucoxanthin-containing dinoflagellates, and only chlorophyll *c2* (one exception) occurred in the peridinin-containing dinoflagellates. These patterns of chlorophyll *c* and major carotenoid correspond to patterns previously observed in the Pyrrophyta and the Chrysophyta, suggesting different phylogenetic origins for the "dinoflagellate" chloroplasts.

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101. Jerome, J.H., R.P. Bukata, and J.E. Bruton, *Utilizing the components of vector irradiance to estimate the scalar irradiance in natural waters*. Applied Optics, 1988. 27(19, 1 Oct.): p. 4012-4018.

Subsurface downwelling and upwelling irradiances are vector quantities, and their measured magnitudes are strongly influenced by the directions of the incident photons. Consequently, they are not the most appropriate parameters for monitoring the energy to which an algal cell or photodegradable contaminant is exposed. A Monte Carlo computer simulation has been used to determine the ratio of the scalar irradiance  $E_0$  to the downwelling irradiance  $E_d$ . These ratios were calculated at depths corresponding to the 100, 10, and 1% downwelling irradiance levels. A range of volume reflectance  $0 < R < 0.14$  was considered, as were six conditions of incident radiation (collimated beams with a range of incident angles plus a diffuse cardioid distribution). Mathematical expressions were curve fitted to the Monte Carlo outputs to yield relationships between  $E$  ratios and  $R$  for the depths and incident conditions considered. It was found that in many cases a single relationship would not accommodate the entire range of volume reflectances and that  $R=0.055$  provided an appropriate demarcation for mathematical curve fitting. Curves, tables, and equations are presented which indicate (a) for all  $R > \sim 0.02$ , the  $E$  ratio at the 1% downwelling irradiance depth is the same for  $\theta = 0$  degrees as for diffuse cardioid incidence, and (b) for  $R > \sim 0.08$ , the  $E$  ratio at the 10% downwelling irradiance depth for  $\theta = 0$  degrees is nearly the same as the  $E$  ratio at the 1% downwelling irradiance depth for diffuse cardioid incidence.

Canada Centre for Inland Waters, National Water Research Institute, Rivers Research Branch, P.O. Box 5050, Burlington, Ontario L7R 4A6.

102. Kiefer, D.A. *Biological sources of optical variability in the sea*. in *Ocean Optics VIII*. 1986. Orlando, FL 637: p. 25-34. SPIE.

Much of the optical variability in the upper sea is caused by variations in the biogenous microparticles, which include the phytoplankton, the Chroococcoid cyanobacteria, and detritus. It is instructive to consider two sources of variability in these biogenous particles. First, changes in the absorption cross section of individual cells result from responses of phytoplankton to the ambient nutrient and light fields. These responses are relatively rapid (days) and a mathematical description of the response is presented. Second, changes in the concentration of detrital particles and cells are more difficult to predict and occur on time scales of weeks. A crude hypothetical model is presented which attempts to describe the general response of the planktonic community to light and nutrient fields. Dept. of Biological Sciences, University of Southern California, Los Angeles CA 90089-0371,

103. Kim, H.H. and H. van der Piepen. *Sunlight Induced 685 NM Fluorescence Imagery*. in *Ocean Optics VIII*. 1986. Orlando, FL 637: p. 358-363. SPIE.

The technique of remote sensing chlorophyll pigment concentrations by monitoring sunlight induced fluorescence at 685 nm is an alternative method of surveying the health and productivity of phytoplankton in the ocean. The 685 nm fluorescence is most intense at the immediate surface and is relatively immune to the presence of sediment or other dissolved products in deeper layers.

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104. Kirk, J.T.O., *Attenuation of light in natural waters*. Australian J. of Marine and Freshwater Res., 1977. 28(4): p. 497-508.

The most relevant characteristics of the incident light field - its intensity, spectral composition and angular distribution - are outlined. The inherent optical properties of the water-absorption coefficient, scattering coefficient, and volume-scattering function are defined, and the contributions of different components of the aquatic system to these are discussed. Taking the properties of the light field and the properties of the water together, the diminution and the change in spectral quality of the light with increasing depth, in different types of water, are considered. The characteristic pattern of attenuation of total photosynthetically active radiation, as measured with a quanta meter, is discussed for inland and coastal waters. CSIRO, Div. of Plant Industry, P.O. Box 1600, Canberra City, A.C.T. 2601, Australia

105. Kirk, J.T.O., *Spectral distribution of photosynthetically active radiation in some south-eastern Australian waters*. Australian J. of Marine and Freshwater Res., 1979. 30(1): p. 81-91.

A study of the spectral distribution of photosynthetically active radiation (PAR) was carried out with a submersible spectroradiometer. There is particularly rapid attenuation with depth of blue light in the 400-500 nm waveband, due to the yellow substances (gilvin and gelbstoff) in the waters. Attenuation in the red region is much less steep than that in the blue. Within the rather shallow euphotic zone typical of these waters the available PAR is impoverished in blue light but still contains plenty of red (630-700 nm) light. At greater depths, in waters of moderate turbidity, a spectral distribution strongly peaked at 580 nm, with a shoulder at 630 nm, is obtained. Suspended soil particles contribute more to vertical light attenuation than does phytoplankton. Direct absorption of light by the particulate inanimate "tripton" is suggested by the data. Turbidity and dissolved color of the water tend to increase together; in particularly turbid, yellow waters the spectral distribution of the PAR is shifted to longer wavelengths. In the clear, comparatively colorless coastal-estuarine waters of Batemans Bay (New South Wales), blue light was attenuated less steeply than red light, so that the underwater spectral distribution, although peaked at 570 nm, was (at 4 m) still quite rich in blue as well as red light.

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106. Kirk, J.T.O., *Estimation of the scattering coefficient of natural waters using underwater irradiance measurements*. Aust. J. Mar. Freshwater Res., 1981. 32(4): p. 533-539.

Certain relationships between irradiance reflectance ( $R$ ), average cosine ( $\mu$ ) and the ratio of the scattering and absorption coefficients, ( $b/a$ ), previously derived by Monte Carlo simulation of underwater light, have been used as the basis for a new method of estimating the scattering and absorption coefficients of natural waters from irradiance measurements made within the water body concerned. Standard curves are presented from which, given  $R$  at a certain optical depth, the values of  $\mu$  at that depth, and  $b/a$  for the water may be read off. The product of  $\mu$  and the vertical attenuation coefficient,  $K_E$ , for net downward irradiance, ( $E_d - E_u$ ), provides an estimate of  $a$ ; this multiplied by  $b/a$  then gives the value for  $b$ . When applied to published data for Lake Pend Oreille the method gives a value for  $b$  differing by only 5% from that which may be calculated by subtracting the absorption coefficient from the beam attenuation coefficient for that lake. Values for scattering coefficient have been calculated by the new method for five water bodies in the southern tablelands of New South Wales for various dates over a 3-year period. The values of  $b$  correlate very closely with nephelometric turbidity, an independent measure of light scattering. The new

procedure gives higher values than those obtained by an earlier method, but is considered to be more accurate.

Division of Plant Industry, CSIRO, P.O. Box 1600, Canberra City, A.C.T. 2601

107. Kishino, M., N. Okami, M. Takahashi, S. Ichimura, *Light utilization efficiency and quantum yield of phytoplankton in a thermally stratified sea*. Limnol. Oceanogr., 1986. 31(3): p. 557-566.

Light utilization efficiency and quantum yield of phytoplankton in a thermally stratified temperate sea were evaluated. Underwater spectral irradiance was measured with a specially designed underwater irradiance meter and the specific absorption coefficient of phytoplankton was determined by a modified opal glass method. The light utilization efficiency of phytoplankton at each depth was derived from photosynthetically fixed energy divided by the energy penetrating into that depth, and quantum yield was estimated from photosynthetic rate divided by quanta absorbed by phytoplankton. Vertical profiles of *in situ* photosynthetic rates per unit volume of water showed two peaks, the first at the depth of about 30% light level (ca. 45,000 cal m<sup>-2</sup> h<sup>-1</sup>) and the second at the depth of about 1.5% light level (ca. 2,500 cal m<sup>-2</sup> h<sup>-1</sup>) with about the same rates. The light utilization efficiency was about 0.5% at the first peak and 5% at the second. The quantum yield was about 0.02 mol C Einst.<sup>-1</sup> at the surface peak and 0.1 at the subsurface peak. The latter value was nearly the same as the maximum yield reported from culture experiments. The Institute of Physical and Chemical Research, Wako-shi, Saitama 351-01 Japan

108. Lasker, R., J. Pelaez, and M. Laurs, *The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy* (*Engraulis mordax*). Remote Sensing of Environment, 1981. 11: p. 439-453.

Using satellite infrared thermal imagery in conjunction with extensive sampling for anchovy eggs and adults during March and April 1980, we were able to confirm that large areas of the coastal ocean off California were avoided by anchovies during the peak of spawning due to entrainment into the California Current of <14 degree C water that upwelled north of Point Conception. Upwelling began coincident with the onset of winds from the north and proceeded in pulses separated by a few days. Plumes of upwelled water appeared to be advected southward in ladder-like rows by the California Current. National Oceanographic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 92038

109. Levandowsky, M., *The use of satellite-based remote sensing for monitoring the brown tide phenomenon*. The Suffolk County Health Services Dept., 1990.

Water samples were collected in two sites near Long Island, NY in 1988, simultaneously with ER2 and EOSAT satellite overflights. Samples were analyzed for species composition and pigments were analyzed by HPLC. Negative correlation of beta-carotene in all bands, particularly with band 4, and the near infrared was noted. The interpretation of this striking result is not yet clear, however.

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110. Lewis, M.R., R.E. Warnock, and T. Platt, *Absorption and photosynthetic action spectra for natural phytoplankton populations: Implications for production in the open ocean*. Limnol. Oceanogr., 1985. 30(4): p. 794-806.

The hypothesis that variation in the initial slope of the photosynthesis-irradiance curve due to variations in the wavelengths of light could be responsible for lower rates of estimated photosynthesis in the open ocean is tested by direct measurement of

photosynthetic action spectra (12-lambda bands, 25 nm bandpass, eight intensities per band) for natural populations from the well mixed waters containing the spring plankton bloom in the Sargasso Sea. We conclude that this possibility is unlikely, at least at this time of year. The spectral shape of *alpha* was similar to that of laboratory diatom or dinoflagellate populations, with a peak at 450 nm, a valley between 500 and 600 nm, and a slight rise at 675 nm. No evidence was found for absorption or photosynthesis by phycobiliproteins and there was little variation with depth. The action spectra covaried with the absorption spectra (determined on glass-fiber filters) except at 400 nm, where higher absorption and relatively little photosynthetic response was observed. Apparent quantum requirements estimated from absorption and action spectra were spectrally invariant (except 400 nm band) and ranged from 600 to 200 moles quanta per mole carbon reduced. It is concluded that estimates of open ocean production from chlorophyll-light models with parameters estimated from laboratory algal cultures are likely to be too high because of a large component of absorption that, while covarying spatially and spectrally with photosynthetic pigment, is itself photosynthetically inactive.

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111. Lewis, M.R. and T.C. Platt. *Remote observation of ocean colour for prediction of upper ocean heating rates*. in *COSPAR, Plenary Meeting, 26th, Topical Meeting on Oceanography from Space*. 1986. Toulouse, France, June 30-July 11: Advances in Space Research. 7(2): p 127-130

The magnitude and variability in the vertical distribution of solar heating of the ocean is controlled by the concentration of pigments imaged by the Coastal Zone Color Scanner. The vertical heating profile influences the thermal structure and dynamics of the upper ocean on time-scales from the diurnal to the climatic, and can potentially be predicted from estimation of attenuation from remote observation of ocean color. Examples are given from a frontal region and the equatorial ocean. It is concluded that such observations would make a significant contribution to outstanding questions of the day in physical oceanography and climate research.

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112. Lewis, M.R., O. Ulloa, and R. Platt, *Photosynthetic action, absorption, and quantum yield spectra for a natural population of Oscillatoria in the North Atlantic*. Limnol. Oceanog., 1988. 33: p. 92-98.

Measurements of the photosynthetic action and absorption spectra were made of marine *Oscillatoria* (*Trichodesmium*) from a summer surface bloom in the North Atlantic. The absorption spectrum was typical of those of other phytoplankton but with small peaks at 627 and 567 nm and a large peak at 493, consistent with the presence of phycocyanin, phycoerythrobilin, and phycourobilin respectively. The photosynthetic action spectrum was determined by measurement of the initial slope of the photosynthesis-irradiance curve every 25 nm from 400 to 675 nm (25 nm bandpass); it was dominated by the phycourobilin waveband. Calculations of quantum yield indicated that it was constant from 475 to 650 nm and was near maximal theoretical values. In wavebands corresponding to chlorophyll absorption (400-450 and 675 nm) quantum yield dropped off sharply. Photosynthesis-irradiance curves determined on both whole colonies and individual trichomes in "white" light indicated that both the initial slope and the degree of photoinhibition at high light were enhanced when the colonies were disrupted - the former by a factor of ten - although the maximum rate of photosynthesis was unchanged. These optical and photosynthetic characteristics of marine *Oscillatoria* are consistent with adaptation to the high light environment where they typically bloom. (Fig. 2 has absorption spectrum on filters.) The phycourobilin chromophore absorption

peak (493 nm) is coincident with the wavelength of maximum transmission in the blue-water regions where *Oscillatoria* is found.

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113. Li, W.K.W., D.V. Subba Rao, W.G. Harrison, J.C. Smith, J.J. Cullen, B. Irwin, and T. Platt, *Autotrophic picoplankton in the tropical ocean*. Science, 1983. 219: p. 292-295.

In phytoplankton of the eastern tropical Pacific Ocean from 25 to 90 percent of the biomass (measured as chlorophyll *a*) and 20 to 80 percent of the inorganic carbon fixation were attributable to particles that could pass a screen with a 1-micrometer pore diameter. Evidence is presented that these are indeed autotrophic cells and not cell fragments.

Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2

114. Malone, T.C., P.G. Falkowski, T.S. Hopkins, G.T. Rowe, and T.E. Whitledge, *Mesoscale response of diatom populations to a wind event in the plume of the Hudson River*. Deep-Sea Res, Part A: Oceanographic Research Papers, 1983. 30(2A): p. 149-170.

Effects of a southwest wind event on distributions of dissolved inorganic nitrogen and diatom biomass are described and evaluated in terms of interactions between circulation, static stability of the water column, and the suspension and growth of diatom populations. A diatom bloom, dominated by *Skeletonema costatum*, developed in response to upwelling as a consequence of the vertical transport of biomass from the aphotic zone (deduced from distributions and rate measurements), a decrease in sinking rate from 1.0 to 0.3 m/d (from sediment trap collections) and lower dilution rates (from hydrography). Carbon-specific growth rate of diatoms showed little variability based on measurements made before and during the bloom, i.e. variations in diatom production were primarily due to variable loss rates rather than to growth. The influence of diatom production associated with the coastal plume of the Hudson River (areas <1000 km<sup>2</sup>) was observed to extend *ca.* 100 km seaward of the zone of most active production. Episodes of cross-shelf transport and onshore accumulation of phytoplankton biomass appear to alternate with periods of high surface production in the plume.

Brookhaven National Lab, Dept. of Energy and Environment, Upton, NY 11973

115. Marra, J., G. Langdon, W.S. Chamberlin, T. Dickey, T. Granata, and D.A. Siegel, *Productivity at the seasonal time scale: An optical view*. Eos, 1990. 71: p. 108.

Considered here are the issues involved in predicting the seasonal primary production in the ocean from optical variables. In 1987, we obtained both shipboard and moored data on biological and optical properties in the Sargasso Sea. Compared to shipboard data, the moored data are highly resolved in time, but limited to 7-8 depths and four bio-optical variables. The data are examined by means of a simple model for primary production at a depth, *z*. The model utilizes (1) the conversion of fluorescence, measured from the mooring; (2) particulate absorption spectra, and (3) direct measurement of scalar irradiance from the mooring. We also show fits to the model of shipboard data from four cruises taken in different seasons.

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(other authors at Dept. of Geological Sciences, USC, and Dept. of Geography UCSB)

116. Maske, H., *The effect of chlorophyll degradation products on the remote sensing signal of natural in vivo fluorescence*, Eos, 1987. 68: p. 1694.

The chlorophyll-specific upwelling radiance signal between 650 and 750 nm is composed of a depression of the elastic backscatter radiance due to absorption by chlorophyll and its derivatives and of natural (daylight-induced) fluorescence. In coastal areas, where

this signal is expected to provide an improved remote sensing signal for phytoplankton, chlorophyll degradation products can constitute half or more of chloro-pigment concentrations. Because they are uncoupled from accessory pigments, the chlorophyll degradation products should have lower specific absorption coefficients than *in vivo* chlorophyll at less than 600 nm. In daylight this will lead to lower natural fluorescence per degraded pigment than per *in vivo* chlorophyll while maintaining similar specific absorption coefficients at 675 nm. Consequently a greater percentage of degraded pigments should lead to decreased fluorescence radiance compared to backscatter depression through absorption. This then constitutes another mechanism inducing a shift of the measured upwelling radiance peak towards longer wavelength.

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117. Mazel, C. *Spectral transformation of downwelling radiation by autofluorescent organisms in the sea*. in *Ocean Optics X*. 1990. Orlando, FL 1302: p. 320-327. SPIE.

The fluorescence emission (685 nm) from chlorophyll in phytoplankton makes a measurable contribution to the upwelling light in the sea. The emissions from other autofluorescing biological sources are not as well described. The photosynthetic accessory pigments (phycoerythrin and phycocyanin) comprise just one additional group of fluorescent substances. Many micro- and macroscopic heterotrophic marine organisms exhibit autofluorescent response to incident radiation over all or part of their surfaces. The intensity may vary widely, and emission wavelengths span the whole visible spectrum. This paper presents microspectrofluorometric measurements of the fluorescence emission from a variety of marine subjects, ranging from single-celled members of the plankton community to both planktonic and attached invertebrates. As modeling of the underwater light field is refined to greater levels of detail, there is need for information on the precise wavelengths of fluorescence emission that might be introduced by biological sources, and on the abundance and distribution of those sources. The existing catalogue of observations of such sources is influenced by the constraints of epifluorescence microscopy and the widespread use of filter sets designed for optimal detection of chlorophyll. With appropriate measurement technique these limitations can be avoided and the catalogue expanded. (Note: phycoerythrin fluoresces at 570-580 nm; phycocyanin at 650-660 nm; heterotrophic dinoflagellates fluoresce green, but spectra have a peak at 475-485 nm.)

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118. McClain, C.R., W.E. Esaias, W. Barnes, B. Guenther, D. Endres, S.B. Hooker, B.G. Mitchell, R. Barnes. *SeaWiFS calibration and validation plan*. 1992. NASA Technical Memorandum 104566, Vol. 3. SeaWiFS Technical Report Series, S.B. Hooker, Editor; Elaine R. Firestone, Technical Editor.

The Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) will be the first ocean color satellite since the Nimbus-7 Coastal Zone Color Scanner (CZCS), which ceased operation in 1986. Unlike the CZCS, which was designed as a proof-of-concept experiment, SeaWiFS will provide routine global coverage every two days and is designed to provide estimates of photosynthetic pigment concentrations of sufficient accuracy for use in quantitative studies of the ocean's primary productivity and biogeochemistry. A review of the CZCS mission is included that describes the limitations of that data set and provides justification for a comprehensive SeaWiFS calibration and validation program. To accomplish the scientific objectives of the mission, the sensor's calibration must be constantly monitored, and robust atmospheric correction and bio-optical algorithms must be developed. The plan incorporates a multi-faceted approach to sensor calibration using a combination of vicarious (based on *in situ* observations) and onboard calibration techniques. Because of budget constraints and the limited availability of ship resources, the development of the operational

algorithms (atmospheric and bio-optical) will rely heavily on collaborations with the Earth Observing Satellite (EOS), the Moderate Resolution Imaging Spectrometer (MODIS) oceans team, and projects sponsored by other agencies, e.g., the United States Navy and the National Science Foundation (NSF). Other elements of the plan include the routine quality control of input ancillary data (e.g. surface wind, surface pressure, ozone concentration, etc., used in the processing and the verification of the level-0 (raw) data to level-1 (calibrated radiances), level-2 (derived products) and level-3 (gridded and averaged derived data) products.

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119. Melack, J.M. and S.H. Pilorz. *Reflectance spectra from eutrophic Mono Lake, California, measured with the Airborne Visible and Infrared Imaging Spectrometer (AVIRIS)*. In *Proceedings of the Second Airborne Visible/Infrared Imaging Spectrometer Workshop*. 1990. Jet Propulsion Laboratory, p. 232-242.

An AVIRIS image was obtained for Mono Lake, California, on 26 May 1989, a day with excellent visibility. Atmospherically-corrected reflectance spectra derived from the image indicate a spectral signature for chlorophyll *a*, the dominant photosynthetic pigment in the phytoplankton of the lake. Chlorophyll *a* concentrations in the lake were about 22 mg m<sup>-3</sup>, and the upwelling radiance was low with a peak reflectance at about 570 nm of about 5%. Coherent noise appeared in the image as regular variations of 0.1 to 0.2  $\mu\text{W cm}^{-2} \text{str}^{-1}$  oriented diagonally to the flight line. A simple ratio of two spectral bands removed the conspicuous undulations, but modifications of the shielding within the instrument are needed to improve the signal, especially over dark targets such as lakes.

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120. Michaelsen, J., X. Zhang, and R.C. Smith, *Variability of pigment biomass in the California Current system as determined by satellite imagery 2. Temporal variability*. J. Geophys. Res., 1988. 93(D9): p. 10,883-10,896.

Characteristics of temporal variability in the California Current system are analyzed using a 30-month time series of Coastal Zone Color Scanner (CZCS) imagery. About 20-25% of the variance is produced by a periodic annual cycle with peak values in winter. Analysis of ship-based chlorophyll measurements indicates that the winter peak is only characteristic of the upper portion of the euphotic zone and that total water column chlorophyll peaks during the spring upwelling season. Satellite studies of intra-annual variability are modulated by strong 5- to 6-day oscillation in the availability of usable imagery, resulting from a combination of satellite orbital dynamics, which produces images of the study area roughly 4 out of every 6 days, and an oscillation in cloud cover which controls the availability of clear imagery. The cloud cover oscillation, which is also present in coastal winds, undoubtedly affects the ocean surface and biases the data obtained by satellites. Analysis of data using a 5-day time step indicates that the predominant mode of nonseasonal variability is characterized by inphase fluctuations throughout the southern and central California coastal region.

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121. Millie, D.F., M.C. Baker, C.S. Tucker, B.T. Vinyard, and C.P. Dionigi. *High-resolution airborne remote sensing of bloom-forming phytoplankton*. J. Phycol. 1992. 28: p. 281-290.

Remote sensing of highly turbid finfish aquaculture impoundments using the Calibrated Airborne Multispectral Scanner (CAMS) mounted on a Lear jet flown at 900 m was



conducted in central Mississippi on 16 May 1990. Concurrent *in situ* data consisted of phytoplankton pigment concentrations and standing crop, water color, turbidity, and surface-water temperature. Surface and near-surface assemblages of cyanophytes and chlorophytes varied dramatically among impoundments; total chlorophyll concentrations and standing crop values ranged from 8 to 483 mg.m<sup>-3</sup> and  $8.0 \times 10^2$  to  $2.2 \times 10^6$  cells per mL, respectively. Regression models fit to CAMS data provided reliable estimates for and produced accurate digital cartographs of total chlorophyll and carotenoid concentrations, phytoplankton standing crop, and turbidity. Although a model to effectively estimate *in situ* c-phycocyanin concentrations was not identified, the lack of a suitable model may have resulted from variability of pigment extraction during quantification rather than failure of remotely sensed imagery to detect c-phycocyanin. Models derived from imagery of impoundments directly beneath the aircraft sufficiently described *in situ* parameters in imagery of adjacent series of impoundments not directly below the aircraft. High-resolution airborne remote sensing provides a means for monitoring local phytoplankton dynamics in temporal and spatial scales analogous to biotic and abiotic processes affecting such dynamics and necessary for applications to ecological research and fisheries or aquacultural management. U.S. Dept. Agriculture, Agricultural Research Service, Southern Regional Research Center, P.O. Box 19687, New Orleans, Louisiana 70179 and Dept. of Biological Sciences, Loyola University, New Orleans, Louisiana 70118

122. Millie, D.F. and G.J. Kirkpatrick. *Investigating the pigment signature of Gymnodinium breve: Are HPLC and remote-sensing technologies applicable for routine monitoring of coastal assemblages?* Aquatic Sciences Meeting, Am. Soc. Limnol. Oceanog. 1992. Santa Fe, NM.

Pigment signatures as determined by High Performance Liquid Chromatography coupled with Photo-diode Array Spectroscopy have been proposed to systematically differentiate between algal phylogenetic groups, and possibly between taxa. Advances in remote-sensing technology have lead to multi-spectral sensors capable of distinguishing spectral reflectance at sensitivities of 2 to 3 nanometers. However, whether these technologies used together can remotely characterize monotypic coastal assemblages remains unproven. As an initial thrust into examining the remote imagery of 'red tide' assemblages, the pigment complex of *Gymnodinium breve* populations acclimated to high-PPFDs with ultraviolet light are examined. Additionally, *in vivo* absorption spectra as linkages between HPLC pigment analyses and spectral reflectance signatures of mono-typic cultures are discussed. Such knowledge of alterations in the pigment signature of *G. breve* will provide necessary information for the accurate interpretation of future remote imagery. In their talk, these authors note that *G. breve* can reach concentrations of  $20 \times 10^6$  cells per liter. Dinoflagellates have Chl *a*, Chl *c*<sub>2</sub> and *c*<sub>3</sub>, as well as fucoxanthin (not peridinin). The chlorophyll:carotenoid ratio decreases in cells grown in bright light, relative to those grown in dim light.

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123. Mitchell, B.G., R. Iturriaga, and D. Kiefer. *Variability of particulate spectral absorption coefficients in the eastern Pacific Ocean.* in *Ocean Optics VII*. 1984. Monterey, CA 489: p.113-118. SPIE.

As part of the Optical Dynamics Experiment (ODEX), the spectral absorption coefficient (440-700 nm) was measured for marine particles sampled at stations in the California current and the eastern edge of the North Central Pacific Gyre. By normalizing the spectral absorption coefficients to the concentration of chlorophyll plus phaeopigments, variability in both the spectral shapes and magnitudes of the specific coefficient can be assessed.

Comparisons between samples indicated large variability vertically (mixed layer versus deep euphotic zone), horizontally (near-shore versus central gyre) and seasonally (fall versus spring).

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124. Mitchell, B.G. and D.A. Kiefer, *Variability in pigment specific particulate fluorescence and absorption spectra in the northeastern Pacific Ocean*. Deep-Sea Research, 1988. 35(5): p. 665-689.

Variability in concentration and type of marine particles is the dominant source of optical variability in the oceans. As part of the Optical Dynamics Experiment (ODEX) spectral absorption coefficients and fluorescence excitation were measured for marine particles sampled at stations in the California Current and the eastern edge of the North Central Pacific Gyre. Chlorophyll *a* normalized fluorescence spectra or chlorophyll *a* plus phaeopigment normalized absorption coefficients were analysed with regard to their spectral shapes and magnitudes. Comparison of absorption samples indicates large variability vertically (mixed layer vs deep euphotic zone), horizontally (nearshore vs central gyre) and seasonally (autumn vs spring). When compared to spectra for detritus and for healthy cultures, it is apparent that a variable fraction of the particulate absorption in the ocean is due to detrital components. The effects of absorption by  $F^*$  exhibited less variability than  $a_p^*$ . Because  $F^*$  appears to be a property of phytoplankton only, the principle causes of variability are photoadaptation and possible taxonomic changes in the phytoplankton crop. Because the origin of particulate organic material (POM) for these regions can be assumed to be derived from *in situ* biogenic processes, the deviation of field spectra from those observed for cultures must in large part be due to the previous history of biological dynamics within a particular water mass. Data presented here indicate that *in situ* or remote optical sensors may be capable of supplying information on algal physiology and ecosystem characterization including the extent of photoadaptation and the accumulation of small detrital particles derived from grazing.

Polar Research Program A-002P, Scripps Institution of Oceanography, La Jolla, CA 92093 and Dept. of Biological Science, University of Southern California, Los Angeles, CA 90089.

125. Mitchell, B.G. and D.A. Kiefer, *Chlorophyll *a* specific absorption and fluorescence excitation spectra for light-limited phytoplankton*. Deep-Sea Research, 1988. 35: p. 639-663.

Methods are described for the measurement of spectral absorption coefficients, fluorescence excitation, and fluorescence yields for pigmented particles retained on filters. The corrections required for absorption coefficients include determining increased optical pathlength while corrections for fluorescence include determining system spectral variability, mean light level and reabsorption. The empirical technique is consistent with and validated by theoretical relationships for light transmission and fluorescence of absorbing particulate material embedded in a medium with intense scattering. These methods were applied to a study of photoadaptation in several phytoplankton species and revealed variations in the blue for chlorophyll *a* specific absorption and fluorescence excitation of greater than 3- to 10-fold respectively. Variations in the spectral shapes and the magnitude of these values with photoadaptation are determined largely by the effect of pigment absorption in discrete particles, sometimes referred to as the sieve or package effect. A model is presented expressing fluorescence in terms which predict large variability in fluorescence due to cell size and cellular pigmentation and which may help reconcile the previously reported, but unexplained variations in fluorescence. Spectral variations in the fluorescence yield appear to be caused by variations in the fraction of light absorbed by photosystem II which fluoresces as compared to photosystem I or photoprotective pigments which do not fluoresce. The

techniques presented provide a rapid, reproducible, and simple approach for routine analysis, particularly for field applications where particle densities are too low for direct analysis of absorption spectra.

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126. Mitchell, B.G. *Algorithms for determining the absorption coefficient of aquatic particulates using the quantitative filter technique (QFT)*. in *Ocean Optics X*. 1990. Orlando, FL 1302: p. 137-148. SPIE.

Particulates in aquatic environments dominate variability in inherent and apparent optical properties. Dilute concentrations have made the quantitative determination of particulate absorption a relatively difficult problem. A quantitative filter technique (QFT) has been described previously, which allows determination of the particulate absorption coefficient for samples concentrated on filters by correcting for the pathlength amplification effect,  $\beta$ . Details of the generality, accuracy and precision of the procedure have not been reported previously. A spectrophotometer equipped with an integrating sphere accessory was used to study the optical density (OD) of phytoplankton suspensions and colored polystyrene beads, and the OD of the same suspensions on a variety of common filter types. The ratio of these two densities confirms that multiple scattering in filters leads to variable  $\beta$ , a non-linear function of the filter OD. Studies of the filter OD when the filters are mounted in different positions in a single spectrophotometer, and for standard and integrating sphere spectrophotometers indicate that the procedures presented are of general applicability. With proper care in baseline correction and sample preparation, spectra can be calculated from measurements of filter optical densities for aquatic particles of diverse size and refractive index with an accuracy of better than  $\pm 15\%$ . A comparison of filter types commonly used for aquatic research indicates that different algorithms are required for estimation of the particulate absorption coefficient from the filter optical density measurements using different filter types. Marine Research Division, A-018, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093-0218

127. Mitchell, B.G., *Predictive bio-optical relationships for polar oceans and marginal ice zones*. J. of Marine Systems, 1992. 3(1-2): p. 91-105.

An analysis of more than 500 stations from polar seas was undertaken to evaluate predictive models linking *in situ* phytoplankton concentrations to measurable optical parameters. The data set consists of profiles of spectral downwelling irradiance, upwelling irradiance, chlorophyll and phaeopigments from 3 cruises to the Antarctic Peninsula, one cruise to the Barents Sea, and one cruise to Fram Strait in the Greenland Sea. The pigment specific diffuse attenuation coefficient for polar regions is significantly smaller, particularly in the blue region of the spectrum, than previous statistical models for temperate oceans predict. Consistent with the observations for the diffuse attenuation coefficient, phytoplankton remote sensing pigment retrieval algorithms, based on upwelling irradiance, show significant differentiation from temperate ocean models. The presently recommended water-leaving radiance algorithm for Coastal Zone Color Scanner data processing underestimates surface pigment concentrations by more than a factor of two for the polar observations reported here. The observations are interpreted in the context of variations in pigment specific particulate absorption which have been described elsewhere. Specifically, the magnitude of pigment specific particulate absorption in the blue is hypothesized to be smaller for polar regions due to significant pigment packaging effects, and a relatively small amount of detrital absorption compared to phytoplankton absorption. Implications for remote sensing of phytoplankton pigments, and pigment-based models of light propagation in the oceans are discussed.

Marine Research Division, A-108, Scripps Institution of Oceanography, San Diego, La Jolla, CA 92093-0218

128. Mitchell, B.G., W.E. Esaias, R.G. Kirk, C.R. McClain, and M.R. Lewis, *Satellite ocean color data for studying oceanic biogeochemical cycles*. in Proceedings, *National Telesystems Conference*, 1991. 1, p. 283-287. 1991. IEEE.

The ocean color mission is a spaceflight mission designed to provide daily, high precision, moderate resolution, multispectral visible observations of global ocean radiance for research biogeochemical processes, climate change, and oceanography. Data delivery will commence in the autumn, 1993. Data will be taken from an ocean color instrument in a near noon sun-synchronous orbit. Local, high-resolution data will be transmitted to the Goddard Space Flight Center (GSFC) for analysis and distribution. The mission established a new paradigm for acquisition of satellite data: NASA will purchase data of a specified quality from a contractor to be selected by a competitive solicitation. The data-buy concept will maximize the entrepreneurial involvement of private industry in satellite-based environmental research. The ocean color mission will provide the first observations of the bio-optical state of the global oceans with sufficient resolution and coverage in space and time to fully characterize the mean and variance of this important aspect of our planet's biosphere. The water leaving radiance data will be used to derive phytoplankton pigments, including chlorophyll-*a*, and to model oceanic primary production and carbon export from the atmosphere through the ocean's photic zone.

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129. Moore, B. and B. Bolin, *The oceans, carbon dioxide, and global climate change*. Oceanus, 1986. 29(4): p. 9.

Four elements, carbon, nitrogen, sulfur and phosphorus, cycle through a closed loop of increasing molecular energy states as the elements are incorporated into living tissue, and then decreasing energy levels as those tissues decompose. These cycles are an expression of life, and constitute the metabolic cycle of the planet. In the absence of significant disturbance, these cycles are in approximate balance of the sources and sinks which result in a quasi steady state. However, human activity since the beginning of the Industrial Revolution has increased to such an extent that it must now be regarded as a significant disturbance to these critical biogeochemical cycles. If we misinterpret even rather minor processes in the ocean, this may have a significant influence on our view on what the likely future partitioning of excess CO<sub>2</sub> will be. The ocean may be slow to respond, but misunderstanding what appear to be minor parameter changes can have costly effects.

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130. Morel, A. and L. Prieur, *Analysis of variations in ocean color*. Limnol. Oceanog., 1977. 22(4): p. 709-722.

Spectral measurements of downwelling and upwelling daylight were made in waters different with respect to turbidity and pigment content and from these data the spectral values of the reflectance ratio just below the sea surface,  $R(\lambda)$  were calculated. The experimental results are interpreted by comparison with the theoretical values computed from the absorption and back-scattering coefficients. The importance of molecular scattering in the light back-scattering process is emphasized. The values observed for blue waters are in full agreement with computed values in which new and realistic values of the absorption coefficient for pure water are used and presented. For the various green waters, the chlorophyll concentrations and the scattering coefficients, as measured, are used in computations which

account for the observed  $R(\lambda)$  values. The inverse process, i.e. to infer the content of the water for measurements at selected wavelengths, is discussed in view of remote sensing applications.

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131. Morel, A. and J. Berthon, *Surface pigments, algal biomass profiles, and potential production of the euphotic layer: Relationships reinvestigated in view of remote-sensing applications*. Limnol. Oceanog., 1989. **34**: p. 1545-1562.

Determinations of time-varying flux of carbon and associated elements in the world ocean is a focused objective of programs such as JGOFS (1988) and IGPB (1988). Photosynthetic carbon fixation by phytoplanktonic algae in the euphotic zone of the ocean remains controversial, but is thought to be comparable to that effected by the terrestrial phytosphere. The temporal and spatial requirements of global monitoring of marine photosynthesis can be met only by satellites, under the proviso that "chlorophyll maps" produced from the data provided by ocean color sensors can be transformed into "production maps". Maps of surface chlorophyllous pigment (Chl *a* + Pheo *a*) are currently produced from ocean color sensors. Transforming such maps into maps of primary production can be reliably done only by using light-production models in conjunction with additional information about the column-integrated pigment content and its vertical distribution. As a preliminary effort in this direction, ~4,000 vertical profiles of pigment (Chl *a* + Pheo *a*) determined only in oceanic Case 1 waters have been statistically analyzed. They were scaled according to dimensionless concentrations (actual concentration divided by the mean concentration within the euphotic layer). The depth  $Z_e$ , generally unknown, was computed with a previously developed bio-optical model. Highly significant relationships were found allowing the pigment content of the euphotic layer to be inferred from the surface concentration observed within the layer of one penetration depth. According to their values (ranging from 0.01 to  $> 10 \text{ mg/m}^3$ ), we categorized the profiles into seven trophic situations and computed a mean vertical profile for each. Between a quasi-uniform profile in eutrophic waters and a profile with a strong deep maximum in oligotrophic waters, the shape evolves rather regularly. The well-mixed cold waters, essentially in the Antarctic zone, have been separately examined. On average, their profiles are featureless, without deep maxima, whatever their trophic state. Averaged values of  $p$ , the ratio of Chl *a* to (Chl *a* + Pheo *a*) have also been obtained for each trophic category. The energy stored by photosynthesizing algae, once normalized with respect to the integrated chlorophyll biomass, is proportional to the available photosynthetic energy at the surface via a parameter which is the cross-section for photosynthesis per unit of areal chlorophyll. By taking advantage of the relative stability of this parameter, we can compute primary production from ocean color data acquired from space. For such computation, inputs are the irradiance field at the ocean surface, the "surface" pigment from which  $\langle C \rangle_{\text{tot}}$  can be derived, the mean  $p$  value pertinent to the trophic situation as depicted by the values, and the cross-section  $\psi$ . Instead of a constant  $\psi$  value, the mean profiles can be used; they allow the climatological field of the  $\psi$  parameter to be adjusted through the parallel use of a spectral light-production model.

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132. Morris, E., ed. *The Physiological Ecology of Phytoplankton*. Studies in Ecology, Vol. 7. 1980, Blackwell Scientific Publications: Oxford.

Chapter Headings: 1. Basic Biological Features of Phytoplankton Cells (F.J.R. Taylor); 2. Problems in the Methodology of Studying Phytoplankton (E. Sakshaug); 3. Light

Attenuation and Phytoplankton Photosynthesis (C.S. Yentsch); 4. The Measurement of Photosynthesis in Natural Populations of Phytoplankton (G.P. Harris); 5. Nitrogen (J.J. McCarthy); Phosphorus (C. Nalewajko & D.R.S. Lean); Silicon (E. Paasche); The Role of Trace Metals in Regulating Phytoplankton Growth (S.A. Huntsman & W.G. Sunda); Vitamins and Phytoplankton Growth (D.G. Swift)

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133. Mueller, J.L. and R.W. Austin. *Ocean optics protocols for SeaWiFS validation*. 1992. NASA Technical Memorandum 104566, Vol.5. SeaWiFS Technical Report Series, S.B. Hooker, Editor; Elaine R. Firestone, Technical Editor. Goddard Space Flight Center, Greenbelt, MD 20771.

This report presents protocols for measuring optical properties, and other environmental variables, to validate the radiometric performance of the Sea-viewing Wide Field-of-View Sensor (SeaWiFS), and to develop and validate bio-optical algorithms for use with SeaWiFS data. The protocols are intended to establish foundations for a measurement strategy to verify the challenging SeaWiFS accuracy goals of 5% in water-leaving radiances and 35% in chlorophyll concentration. The protocols first specify the variables which must be measured, and briefly review rationale. Subsequent chapters cover detailed protocols for instrument performance specifications, characterizing and calibrating instruments, methods of making measurements in the field, and methods of data analysis. These protocols were developed at a workshop sponsored by the SeaWiFS Project Office (SPO) and held at the Naval Postgraduate School in Monterey, California (9-12 April 1991). This report is the proceedings of that workshop, as interpreted and expanded by the authors and reviewed by workshop participants and other members of the bio-optical research community. The protocols are a first prescription to approach unprecedented measurement accuracies implied by the SeaWiFS goals, and research and development are needed to improve the state-of-the-art in specific areas. The protocols should be periodically revised to reflect technical advances during the SeaWiFS Project cycle.

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134. Mueller, J.L., C.C. Trees, and R.A. Arnone. *Evaluation of Coastal Zone Color Scanner diffuse attenuation coefficient algorithms for application to coastal waters*. in *Ocean Optics X*. 1990. Orlando, FL 1302: p.72-78. SPIE.

The Coastal Zone Color Scanner (CZCS) and associated atmospheric and in-water algorithms have allowed synoptic analyses of regional and large scale variability of bio-optical properties [phytoplankton pigments and diffuse attenuation coefficient  $K(490)$ ]. Austin and Petzold (1981) developed a robust in-water  $K(490)$  algorithm which related the diffuse attenuation coefficient at one optical depth [ $1/K(490)$ ] to the ratio of the water-leaving radiances at 443 and 550 nm. The regression analyses included diffuse attenuation coefficients  $K(490)$  up to  $0.40\text{ m}^{-1}$ , but excluded data from estuarine areas, and other Case II waters, where the optical properties are not predominantly determined by phytoplankton. In these areas, errors are induced in the retrieval of remote-sensing  $K(490)$  by extremely low water-leaving radiance at 443 nm and improved accuracy may be realized by using algorithms based on wavelengths where  $L(\lambda)$  is larger. Using ocean optical profiles acquired by the Visibility Laboratory, algorithms are developed to predict  $K(490)$  from ratios of water leaving radiances at 520 and 670, as well as 443 and 550 nm.

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135. Nelson, N.B., B.B. Prezelin, and R.R. Bidigare, *Phytoplankton light absorption and the package effect in California coastal waters*. Mar. Ecol. (Prog. Ser.), 1993. **94**: p. 217-227.

Phytoplankton absorption spectra were determined for communities collected in the upper euphotic zone over a 250 km transect across a highly variable region of the Southern California Bight. The influence of the 'package effect' on phytoplankton spectra was assessed by comparison of absorption coefficient spectra based on direct measurements with spectral reconstructions calculated from HPLC-determined pigment concentrations. Measurable package effect occurred in less than 25% of samples, principally from samples taken in the subsurface chlorophyll *a* maximum layer and in association with populations of large diatoms or dense prymnesiophyte concentrations. Estimates of the package effect in the field derived from these measurements were consistent with the majority of laboratory-determined data for chromophyte and chlorophyte algae. In the cases where reconstructed phytoplankton absorption spectra overestimated measured spectra, the majority of differences could be reconciled by application of an algorithm calculating the package effect. Where package effects were minimal, reconstructed absorption spectra provided accurate estimates of phytoplankton photosynthetic light absorption without correction for package effects. Existing models for phytoplankton absorption properties will benefit from inclusion of information on the package effect, determined from direct absorption measurements or from information on the taxonomic composition of the phytoplankton community.

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136. Olson, R.J., S.W. Chisholm, E.R. Zettler, and E.V. Armbrust, *Pigments, size, and distribution of Synechococcus in the North Atlantic and Pacific Oceans*. Limnol. Oceanogr., 1990. **35**(1): p. 45-58.

Dual-beam flow cytometry was used to analyze the distribution and optical characteristics of *Synechococcus* in the North Atlantic and Pacific Oceans. The depth range over which *Synechococcus* cells were abundant was related to the depth of the nitrite maximum and the chlorophyll maximum, but was not significantly correlated with the depth of the surface isothermal layer. Dual-beam analysis of chromophore pigment types revealed that the majority of the populations were of the high-urobilin type; low-urobilin types were found only in coastal waters where they almost always co-occurred with high-urobilin strains. Phycoerythrin fluorescence intensity per cell increased dramatically with depth in the lower euphotic zone at all stations; at some open-water stations, very deep cells were as much as 100 times brighter than those at the surface. The maximal fluorescence per cell was about the same at the coastal and oceanic stations, and the depth of maximal fluorescence was closely related to the depth of the nitrite maximum. At most stations, fluorescence per cell was constant throughout the mixed layer, but at some open stations it decreased continuously to the surface. The latter pattern suggests that mixing rates in these areas are slow relative to the abilities of the cells to photoacclimate. A distinct diel pattern in forward-angle light scatter was observed in cells in the mixed layer over vast regions, which we hypothesize to be coupled to growth of the cells during daylight hours. Absorptive properties of these high-phycoerythrin strains are not very different from those of the eucaryotic phytoplankton because they have a strong absorption peak at about 495 nm in addition to the 545-nm absorption peak of phycoerythrobilin. This pigment complement could explain why photosynthetic action spectra measured in oceanic waters do not yield the patterns one would expect from cells containing mainly phycoerythrobilin.

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137. Ondrusek, M.E., R.R. Bidigare, S.T. Sweet, D.A. Defreitas, and J.M. Brooks, *Distribution of phytoplankton pigments in the North Pacific Ocean in relation to physical and optical variability*. Deep-Sea Research, 1991. 38(2): p. 243-266.

To investigate phytoplankton distributions in the North Pacific Ocean, samples of suspended particulate material were collected from the upper 300 m during two cruises in 1985 for detailed analysis of algal pigments by high-performance liquid chromatography (HPLC). Transpacific Leg I, along 24° N in April and May, crossed three prominent hydrographic features: the California Coastal Current, the North Pacific Central Gyre and the Kuroshio Current. Transpacific Leg II, along 47° N in August and September, crossed the Kuroshio extension, the Subarctic Gyre and the North Pacific Current. Individual pigments were partitioned vertically in the water column, showing distinct spatial patterns across the Pacific Ocean which reflected the large-scale circulation. Vertical distributions of phytoplankton pigments displayed consistent patterns over spatial scales of thousands of kilometers. In near-surface, nitrate-rich waters, fucoxanthin was the dominant carotenoid. In nitrate-poor surface waters, zeaxanthin was the dominant carotenoid at the surface, and 19'-hexanoylfucoxanthin and chlorophyll *b* concentrations were elevated near the base of the euphotic zone. Phaeopigment concentrations greater than a few tens of nanograms per liter were never encountered. Based on Principal Component Analysis, stations clustered into three general pigment categories which followed specific hydrographic characteristics of oligotrophic, highly productive and transitional regions. (Note from EW: these vertical distributions will be very important in interpreting ocean color.)

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138. Paerl, H.W., *Nuisance phytoplankton blooms in coastal, estuarine, and inland waters*. Limnol. Oceanogr., 1988. 33(4 (part2)): p. 823-847.

Multiple interacting physical, chemical, and biotic factors, in proper combination, lead to the development and persistence of nuisance algal blooms. Upon examining combinations of environmental conditions most likely to elicit nuisance blooms, commonalities and analog situations become more apparent among coastal marine (dinoflagellate-dominated), estuarine (dinoflagellate- and cyanobacteria-dominated) and freshwater (cyanobacteria-dominated) ecosystems. A combination of the following hydrological, chemical, and biotic factors will most likely lead to bloom-sensitive waters: a horizontally distinct water mass; a vertically stratified water column; warm weather conditions, as typified by dry monsoon tropical climates and summer seasons in temperate zones; high incident photosynthetically active radiation (PAR); enhanced allochthonous organic matter loading (both as DOC and POC); enhanced allochthonous inorganic nutrient loading (nitrogen and/or phosphorus); adequate availability of essential metals, supplied by terrigenous inputs or upwelling; underlying sediments physically and nutritionally suitable as "seed beds" for resting cysts and akinetes; algal-bacterial synergism, which exhibits positive impacts on phycosphere nutrient cycling; algal-micrograzer (protists and rotifers) synergism, which also enhances nutrient cycling without consumption of filamentous and colonial nuisance taxa; and selective (for non-nuisance taxa) activities of macrograzers (crustacean zooplankton, larval fish). Nuisance bloom taxa share numerous additional physiological and ecological characteristics, including limited heterotrophic capabilities, high degrees of motility, and toxicity. Given such a set of commonalities, it would appear useful and timely to identify and address generally applicable criteria for deeming a water body "bloom sensitive" and to incorporate such criteria into the design of water quality management strategies applicable to both coastal marine and freshwater habitats.

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139. Paerl, H.W. J. Rudek, and M.A. Mallin, *Stimulation of phytoplankton production in coastal waters by natural rainfall inputs: nutritional and trophic implications*. Marine Biology, 1990. 107: p. 247-254.

Recent evaluations of estuarine and coastal nutrient budgets implicate atmospheric deposition as a potentially significant (20 to 30%) source of biologically available nitrogen. We examined the potential growth stimulating impact of atmospheric nitrogen loading (ANL) as local rainfall, in representative shallow, nitrogen limited North Carolina mesohaline estuarine and euhaline coastal Atlantic Ocean habitats. From July 1988 to December 1989, using *in situ* bioassays, we examined natural phytoplankton growth responses, as  $^{14}\text{CO}_2$  assimilation and chlorophyll *a* production, to rain additions over a range of dilutions mimicking actual input levels. Rainfall at naturally occurring dilutions (0.5 to 5%) stimulated both  $^{14}\text{CO}_2$  assimilation and chlorophyll *a* production, in most cases in a highly significant manner. Parallel nutrient enrichments consistently pointed to nitrogen as the growth stimulating nutrient source. Generally, more acidic rainfall led to greater magnitudes of growth stimulation, especially at lower dilutions. Nutrient analyses of local rainfall from May 1988 to January 1990 indicated an inverse relationship between pH and  $\text{NO}_3^-$  content. There have been growing concerns regarding increasing coastal and estuarine eutrophication, including ecologically and economically devastating phytoplankton blooms bordering urban and industrial regions of North America, Europe, Japan, and Korea. It appears timely, if not essential, to consider atmospheric nutrient loading in the formulation and implementation of nutrient management strategies aimed at mitigating coastal eutrophication. Hitherto unseen symptoms of nutrient related accelerated eutrophication have, during the past decade, appeared in previously bloom-free North Carolina coastal rivers and oligohaline estuaries. Included are massive blooms of the cyanobacterial nuisance genera *Anabaena*, *Aphanizomenon*, and *Microcystis*. In adjacent coastal waters the first ever recorded toxic bloom of the "red tide" dinoflagellate *Ptychodiscus brevis* devastated shellfish and finfish industries, recreational fishing, and tourism. Other examples of recent disastrous blooms of toxic or undesirable algae and cyanobacteria in many parts of the world previously free of them are given. The proximity of the same coastal waters to enhanced atmospheric nitrogen loading makes them susceptible to unusually high rates of eutrophication. The synergism of physical, chemical, and biotic interactions potentially linking atmospheric nitrogen loading to accelerated eutrophication in diverse marine systems requires urgent research and management attention.

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140. Paerl, H.W., *Physiological ecology and regulation of  $\text{N}_2$  fixation in natural waters*, in *Advances in Microbial Ecology*, K.C. Marshall, Editor. 1990, Plenum Publishing: p. 305-344.

Biological nitrogen fixation, the nitrogenase-catalyzed process by which certain procaryotes reduce atmospheric dinitrogen ( $\text{N}_2$ ) is of fundamental importance in mediating the availability of utilizable nitrogen in the biosphere. This process is of particular relevance in ecosystems exhibiting deficiencies in nitrogen availability; in this regard, it is well established that geographically and trophically diverse freshwater lakes, rivers, and reservoirs as well as estuarine, coastal, and oceanic habitats exhibit chronic nitrogen deficiencies. Among these waters, newly formed combined nitrogen inputs attributable to  $\text{N}_2$  fixation may regulate productivity and fertility. (This excellent review has sections on aquatic  $\text{N}_2$ -fixing microorganisms, their diversity and habitats; the physiological ecology of aquatic nitrogen fixation; environmental constraints and limitations on aquatic nitrogen fixation; role of organic

matter and microzone formation; and evolutionary and ecological considerations. The conclusion: striking similarities exist in the range of habitats amenable or prohibitory to the establishment and proliferation of N<sub>2</sub>-fixing microorganisms among diverse freshwater and marine habitats. Physical, chemical, and biotic constraints on N<sub>2</sub> fixation appear similar across salinity gradients. From a biogeochemical perspective, the degree to which N<sub>2</sub>-fixation can supply nitrogen requirements plays a key role in determining the trophic state and fertility in individual aquatic environments, regardless of salinity. Institute of Marine Sciences, University of North Carolina, Chapel Hills, Morehead City, North Carolina 28557

141. Paerl, H.W., *Ecophysiological and trophic implications of light-stimulated amino acid utilization in marine picoplankton*. Applied and Environmental Microbiology, 1991. 57(2): p. 473-479.

By using microautoradiography, light-stimulated utilization of dissolved amino acids for natural marine phytoplankton assemblages was demonstrated. The <2- $\mu$ m diameter picoplankton, known to be a dominant fraction of marine primary production, revealed a widespread capability for this process. Autofluorescent (chlorophyll *a* -containing) picoplankton and some larger phytoplankton from diverse oceanic locations, as well as isolates of the representative cyanobacterial picoplankton *Synechococcus* spp., showed light-stimulated incorporation of amino acids at trace concentrations. Dark-mediated amino acid utilization was dominated by nonfluorescent bacterial populations. Among autofluorescent picoplankton, light-stimulated exceeded dark-mediated amino acid incorporation by 5 to 75%; light-stimulated amino acid incorporation was only partially blocked by the photosystem II inhibitor DCMU, suggesting a photoheterotrophic incorporation mechanism. Parallel light versus dark incubations with glucose and mannitol indicated a lack of light-stimulated utilization of these non-nitrogenous compounds. Since marine primary production is frequently nitrogen limited, light-mediated auxotrophic utilization of amino acids and possibly other dissolved organic nitrogen (DON) constituents may represent exploitation of the relatively large DON pool in the face of dissolved inorganic nitrogen depletion. This process increases the efficiency of DON retention at the base of oceanic food webs and may in part be responsible for relatively high rates of picoplankton production under conditions of chronic dissolved inorganic nitrogen limitation. Picoplanktonic recycling of organic matter via this process has important ramifications with respect to trophic transfer via the "microbial loop". Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, North Carolina 28557

142. Paerl, H.W. and D.F. Millie. *Evaluations of spectrophotometric, Fluorometric and high performance liquid chromatographic methods for algal pigment determinations in aquatic ecosystems*. 1991. United States Environmental Protection Agency.

Summary: A workshop entitled "Evaluations of Spectrophotometric, Fluorometric, and High Performance Liquid Chromatographic Methods For Algal Pigment Determinations in Aquatic Ecosystems" was convened at Duke University on 4 August 1991 to examine and evaluate analytical issues, recent technological advances, and applications of these technologies in quantitative and qualitative assessments of algal production, community composition, and systematics. Algal pigment experts, phycologists, limnologists, and oceanographers provided recommendations concerning water sampling, pigment extraction and processing, and high performance liquid chromatographic (HPLC) protocols. Specifically, applicabilities of pigment analyses for estimating algal biomass and community composition, identifying phylogenetic distinctions among algae, and examining trophic processes within aquatic systems were identified. Additionally, the relationship between algal spectral

reflectance signature, pigment absorbance spectra, and HPLC as means to monitor algal production, trophic and water quality status, and biogeochemical processes on local, regional, and global scales were discussed. In this regard, current and future ecosystem-level applications of HPLC-photodiode array spectrophotometry, flow cytometry coupled to fluorescence detection and remote sensing were evaluated.

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143. Peacock, T.G., K.L. Carder, C.O. Davis, and R.G. Steward, *Effects of fluorescence and water Raman scattering on models of remote sensing reflectance*. in *Ocean Optics X*. 1990. Orlando, FL 1302: p. 303-319. SPIE.

The modeling of oceanic remote sensing reflectance typically employs absorption and scattering parameters for the various constituents present in marine waters. Trans-spectral light sources such as fluorescence and Raman scattering are not generally parameterized in these models. Bioluminescence is not considered to be a significant contributor to water-leaving radiance measurements obtained mid-day, and has not been included in the models either. In this paper we present evidence of effects due to these three phenomena by comparing model results to remote sensing reflectances measured at several stations during the 1988 California Coastal Transition Zone (CTZ) Experiment. Differences between modeled and measured  $R_{rs}(\lambda)$  values are discussed from the perspective of *in-situ* light source contributions. Conclusion states that "Recent studies indicate a Raman contribution to water-leaving radiance of up to about 13% in low pigment waters."

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144. Pelaez, J. and J. McGowan, *Phytoplankton pigment patterns in the California Current as determined by satellite*. *Limnol. Oceanogr.*, 1986. 31(5): p. 927-950.

The satellite images of phytoplankton pigments off California show a high degree of heterogeneity. However, recurrent phytoplankton pigment structures can be identified in the California Current. The major ones are: two sharp boundaries several hundreds of kilometers long; low pigment eddies far offshore interwoven with higher pigment structures immediately inshore; a low pigment intrusion in the Southern California Bight, and a higher pigment region farther offshore; eddies "attached" to shallow coastal areas; and California Current rings spawned far offshore. The larger scale structures of phytoplankton pigments show a remarkable continuity throughout a year, but there is shifting, wobbling, and erosion of these structures. The structures are strong and distinct in spring and summer, weaken through fall (except for a slight intensification in October) and become weakest and poorly defined in late fall-early winter. The patterns of distribution of phytoplankton pigments for a given season tend to reappear from one year to another during the 3 years analyzed. Such recurrency is significant because these patterns may change, and some disappear within any given year. Clear similarities of the phytoplankton pigment distributions to the field of dynamic height and to an infrared image of sea surface temperature indicate the very important role of ocean circulation and of phytoplankton nutrient content of the waters, in the generation and maintenance of the observed patterns.

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145. Perry, M.J. and S.M. Porter, *Temporal changes in the relative contribution of major phytoplankton groups to absorption in the Sargasso Sea*. *Eos*, 1990. 71(2): p. 109.

Chlorophyll and phycoerythrin fluorescence of individual cells was analyzed with a Coulter EPICS flow cytometer during the 1987 Biowatt program in May, August, and

December. Fluorescence was excited with an argon laser tuned to 488 nm. Based on flow cytometric fluorescence, phytoplankton could be classified into three broad categories: cyanobacteria, pro-chlorophytes, and eukaryotes. An empirical relationship between fluorescence (stimulated by 488 nm light) and absorption per cell at 488 nm was used to compute the absorption cross section of individual phytoplankton cells. The regression equation for the absorption cross section yielded the Chl *a* fluorescence per cell. The relative contribution to the total phytoplankton absorption coefficient by each of the three classes of phytoplankton varied with depth and season and was often dominated by the cyanobacteria. A few large eukaryotic cells contributed disproportionately to the total absorption coefficient and, by inference, should also contribute disproportionately to primary production.

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146. Phillips, D.M. and J.T.O. Kirk, *Study of the spectral variation of absorption and scattering in some Australian coastal waters*. Australian J. Mar. Freshwat. Res., 1984. **35**(6): p. 635-644.

The spectral variation of absorption and scattering of sea water in Jervis Bay on the east coast of Australia has been studied over the wavelength range from 400 to 700 nm. The absorption and scattering coefficients were derived from measurements of the beam attenuation coefficient and the vertical attenuation coefficient for downwelled irradiance using an empirical relationship based on Monte Carlo calculations. The results indicate that scattering is essentially independent of wavelength whereas absorption due to suspended and dissolved matter increases rapidly at short wavelengths. The relative contribution of absorption to total attenuation is smaller for Jervis Bay waters than for the waters of Gulf St. Vincent, South Australia.

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147. Phinney, D.A. and C.S. Yentsch. *The relationship between phytoplankton concentration and light attenuation in ocean waters*. in *Ocean Optics VIII*. 1986. Orlando, FL **637**; p. 321-327. SPIE.

The accuracy of chlorophyll estimates by ocean color algorithms is affected by the variability of particulate attenuation, the presence of dissolved organic matter and the non-linear inverse relationship between the attenuation coefficient, *K*, and chlorophyll. Data collected during the Warm Core Rings Program were used to model the downwelling light field and determine the impact of these errors. A possible mechanism for the non-linearity of *K* and chlorophyll is suggested, namely, that changing substrate from nitrate-nitrogen to ammonium causes enhanced blue absorption by photosynthetic phytoplankton in oligotrophic surface waters.

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148. Phinney, D.A., C.S. Yentsch, and J. Rohrer. *Three color laser fluorometer for studies of phytoplankton fluorescence*. in *Ocean Optics IX*. 1988. Orlando, FL **925**; p. 171-175. SPIE.

A three color laser fluorometer has been developed for field work operations. Using two tunable dye lasers (excitation wavelengths at 440 nm and 530 nm) broadband wavelength optical filters were selected to obtain maximum fluorescence sensitivity at wavelength >675 (chlorophyll) and 575 nm ( $\pm 15$  nm (phycoerythrin)). The laser fluorometer permits the measurement of phytoplankton pigments under static or flowing conditions and more closely resembles the time scales (ns) and energy levels (mW) of other laser-induced fluorescence instruments.

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149. Pilon, S.H. and C.O. Davis. *Investigations of ocean reflectance with AVIRIS data. In Second Airborne Visible/Infrared Imaging Spectrometer Workshop*. 1990. Jet Propulsion Laboratory. p. 224-231.

Multispectral imagery with the resolution of the Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) offers the possibility for retrieving concentrations of in-water constituents in turbid and coastal waters inaccessible to instruments of low spectral and spatial resolution. The oceanography group at the Jet Propulsion Laboratory (JPL) is involved in an ongoing experiment at Monterey Bay, California, coupling AVIRIS overflights with *in-situ* data for development of spectral unmixing algorithms suitable for AVIRIS and the High Resolution Imaging Spectrometer (HIRIS). Given the low signal emitted by water, a large portion of the developmental work has centered on defining signal-to-noise characteristics necessary for separation of spectral endmembers. Although AVIRIS was not originally designed for ocean viewing, several improvements have been made in the data processing and acquisition, as well as to the instrument itself, which put AVIRIS on the borderline of detection requirements for estimation of chlorophyll concentrations. Further modifications have been proposed which would increase the S/N by a factor of 2 to 4 in the blue regions of the spectrum enabling use of the instrument for spectral unmixing of pigments, chlorophyll, and suspended sediments. This paper documents the present capabilities of AVIRIS for ocean studies and quantifies the need for improved S/N in the visible part of the spectrum.

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150. Platt, T. and K. Denman, *Patchiness in phytoplankton distribution*, in *The Physiological Ecology of Phytoplankton*, I. Morris, Editor. 1980, University of California Press: Berkeley and Los Angeles. p. 413-431.

Sections: Introduction, A working hypothesis for phytoplankton patchiness, Scales of patchiness, Methodology in patchiness studies, Typical power spectra and physical theories of patchiness, Biophysical theories of patchiness, Vertical effects, Other factors known to influence patchiness, Significance of phytoplankton patchiness in the food chain, Broader implications, and References.

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151. Platt, T. and A.W. Herman, *Remote sensing of phytoplankton in the sea-surface-layer chlorophyll as an estimate of water-column chlorophyll and primary production*. *Int. J. of Remote Sensing*, 1983. 4(Apr-June): p. 343-351.

The utility of remotely-sensed chlorophyll data in biological oceanography is assessed. Oceanographic data, highly resolved in the vertical, are used as a basis for estimating the (weighted) proportion of the water-column chlorophyll that is accessible to the remote sensor. Examples are calculated for the continental shelf off Nova Scotia, the Canadian Arctic and the coast of Peru. The analysis is extended to the estimation of phytoplankton production. Remotely-sensed data contain only a small (5 percent of phytoplankton biomass and 11 percent of the turnover), but a surprisingly stable fraction of the information for the water column. A modest ground-truthing program is required to exploit these data to the best advantage.

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152. Platt, T., D.V. Subba Rao, and B. Irwin, *Photosynthesis of picoplankton in the oligotrophic ocean*. Nature, 1983. 301(24 Feb.): p. 702-704.

Against a background of controversy concerning the absolute magnitude of biological productivity in the oligotrophic, tropical ocean, evidence is accumulating for the existence there of a population of minute, unicellular organisms collectively known as picoplankton. In the tropical Pacific, it has been estimated recently that cells passing a 1  $\mu\text{m}$  screen (picoplankton) make a very substantial contribution to the rate of turnover of phytoplankton biomass. On the other hand, previous work in the tropical Atlantic led to the conclusion that particles in the size class  $<3 \mu\text{m}$  are fragments of larger cells and metabolically inert. We present here the first data on the photosynthetic characteristics of picoplankton collected at sea. This new evidence from the tropical North Atlantic supports the argument that the picoplankton contains a significant, metabolically-active, autotrophic component, capable of supplying about 60% of the total primary production in an open-ocean ecosystem. (Average light available at the chlorophyll maximum during an 11 h light day is  $\sim 6 \text{ W/m}^2$ .)

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153. Platt, T. and S. Sathyendranath, *Oceanic primary production: estimation by remote sensing at local and regional scales*. Science, 1988. 241: p. 1613-1620.

Satellites provide the only avenue by which marine primary production can be studied at ocean-basin scales. With maps of chlorophyll distribution derived from remotely sensed data on ocean color as input, deduction of a suitable algorithm for primary production is a problem in applied plant physiology. An algorithm is proposed that combines a spectral and angular model of submarine light with a model of the spectral response of algal photosynthesis. To apply the algorithm at large horizontal scale, a dynamic biogeography is needed for the physiological rate parameters and the biological structure of the water column. Fieldwork to obtain this type of data should be undertaken so that the use of satellite data in modern biological oceanography may be optimized.

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154. Platt, T. and S. Sathyendranath, *Biological production models as elements of coupled, atmosphere-ocean models for climate research*. J. Geophys. Res., 1991. 96(Feb. 15): p. 2585-2592.

Process models of phytoplankton production are discussed with respect to their suitability for incorporation into global-scale numerical ocean circulation models. Exact solutions are given for integrals over the mixed layer and the day of analytic, wavelength-independent models of primary production. Within this class of model, the bias incurred by using a triangular approximation (rather than a sinusoidal one) to the variation of surface irradiance through the day is computed. Efficient computation algorithms are given for the nonspectral models. More exact calculations require a spectrally sensitive treatment. Such models exist, but must be integrated numerically over depth and time. For these integrations, resolution in wavelength, depth, and time are considered and recommendations made for efficient computation. The extrapolation of the one-(spatial)-dimension treatment to large horizontal scale is discussed.

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155. Prezelin, B.B. and H.A. Matlick, *Primary production in marine snow during and after an upwelling event*. Limnol. Oceanogr., 1983. 28(6): p. 1156-1167.

Marine snow (flocculent macroscopic particles) collected during an upwelling event near Santa Barbara, California, was recently formed and inhabited by phytoplankton physiologically similar to those free-living in the water. At least 20% of all primary production, Chl *a* and phytoplankton occurred on this marine snow, suggesting that a significant fraction of new organic carbon entering the upwelling food chain is available to large-particle feeders or passes directly through the detrital food chain on particles. In contrast, marine snow collected 2 weeks after the upwelling event was inhabited by a physiologically distinct community of aging, senescent, phytoplankton: <1% of total primary production and Chl *a* occurred on this marine snow. High dark fixation rates, high RUBPCase activity on photosynthetically depressed snow, and high ammonium concentrations within this snow suggest that chemotrophic bacteria, possibly nitrifying bacteria may be particularly active on these macroscopic particles.

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156. Prezelin, B.B., M. Putt and H.E. Glover, *Diurnal patterns in photosynthetic capacity and depth-dependent photosynthesis-irradiance relationships in Synechococcus spp. and larger phytoplankton in three water masses in the Northwest Atlantic Ocean*. Mar. Biol., 1986. 91(2): p.207-217

The photosynthetic characteristics of prokaryotic phycoerythrin-rich populations of cyanobacteria *Synechococcus* spp. and larger eukaryotic algae were compared at a neritic frontal station (P1), in a warm-core eddy (P2), and at Wilkinson's Basin (P3) during a cruise in the Northwest Atlantic Ocean in the summer of 1984. *Synechococcus* spp. numerically dominated the 0.6 to 1  $\mu\text{m}$  fraction, and to a lesser extent the 1 to 5  $\mu\text{m}$  size fractions, at most depths at all stations. At P2 and P3, all three size categories of phytoplankton (0.6 to 1  $\mu\text{m}$ , 1 to 5  $\mu\text{m}$ , and >5  $\mu\text{m}$ ) exhibited similar depth-dependent changes in both the timing and amplitude of diurnal periodicities of chlorophyll-based and cell-based photosynthetic capacity. Mid-day maxima in photosynthesis were observed in the upper water column which damped out in all size fractions sampled just below the thermocline. For all size fractions sampled near the bottom of the euphotic zone, the highest photosynthetic capacity was observed at dawn. At all depths, the *Synechococcus* spp.-dominated size fractions had lower assimilation rates than larger phytoplankton size fractions. This observation takes exception with the view that there is an inverse size-dependency in algal photosynthesis. Results also indicated that the size-specific contribution to potential primary production in surface waters did not vary appreciably over the day. However, estimates of the percent contribution of *Synechococcus* spp. to total primary productivity in surface waters at the neritic front were significantly higher when derived from short-term incubator measurements of photosynthetic capacity rather than from dawn-to-dusk *in situ* measurements of carbon fixation. The discrepancy was not due to photoinhibitory effects on photosynthesis, but appeared to reflect increased selective grazing pressure on *Synechococcus* spp. in dawn-to-dusk samples. Low-light photoadaptation was evident in analyses of the depth-dependency of P-I parameters (photosynthetic capacity,  $P_{\text{max}}$ ; light-limited slope,  $\alpha$ ;  $P_{\text{max}} \alpha$ ,  $I_k$ ; light-intensity beyond which photoinhibition occurs,  $I_b$ ) of the >0.6  $\mu\text{m}$  communities at all three stations and was attributable to stratification of the water column. There was a decrease in assimilation rates and  $I_k$  with depth that was associated with increases in light-limited rates of photosynthesis. No mid-day photoinhibition of  $P_{\text{max}}$  or  $I_b$  was observed in any surface station. Marked photoinhibition was detected only in the chlorophyll maximum at the neritic front and below the surface mixed-layer at Wilkinson's Basin, where susceptibility to photoinhibition increased with the depth of the collected sample. The 0.6 to 1  $\mu\text{m}$  fraction always had lower light requirements for light-saturated photosynthesis than the >5  $\mu\text{m}$  size fraction within the same sample. Saturation intensities for the 1 to 5  $\mu\text{m}$  and 0.6 to 1  $\mu\text{m}$  size fractions were

more similar when *Synechococcus* spp. abundances were high in the 1 to 5  $\mu\text{m}$  fraction. The  $>5$   $\mu\text{m}$  fraction appeared to be the prime contributor to photoinhibitory features displayed in mixed samples ( $>0.6$   $\mu\text{m}$ ) taken from the chlorophyll maxima. In *Synechococcus* spp.-dominated 0.6 to 1 and 1 to 5  $\mu\text{m}$  size fractions, cellular chlorophyll *a* content increased 50- to 100-fold with depth and could be related to increases in maximum daytime rates of cellular  $P_{\text{max}}$  at the base of the euphotic zone. Furthermore, the 0.6 to 1  $\mu\text{m}$  and  $>5$   $\mu\text{m}$  fractions sampled at the chlorophyll maximum in the warm-core eddy had lower light requirements for photosynthesis than comparable surface samples from the same station. Results suggest that photoadaptation in natural populations of *Synechococcus* spp. is accomplished primarily by changing photosynthetic unit number, occurring in conjunction with other accommodations in the efficiency of photosynthetic light reactions.

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157. Prezelin, B.B. and B.A. Boczar, *Molecular bases of cell absorption and fluorescence in phytoplankton: potential applications to studies in optical oceanography.*, in *Progress in Phycological Research*, F. Round and D. Chapman, Editors. 1986, Elsevier Science Publishers; Biopress Ltd.: p. 350-465.

This extensive review is a treasure trove of information, with numerous illustrations. Pertinent for this paper are the following remarks: Remote-sensed fluorimetric estimates of chlorophyll are possible. The red chlorophyll fluorescence emission peak is detectable as a 685 nm peak in radiance reflectance spectra (upwelling radiance/downwelling irradiance) in highly productive waters. The signal can be increased in less productive waters by using airborne laser light rather than sunlight to excite pigment fluorescence. LIDAR (light detection and ranging) fluorosensor uses a garnet and/or excimer dye laser to pulse the sea surface respectively with 532 nm or 427 nm light, the first wavelength primarily exciting accessory carotenoids (fucoxanthin and peridinin) and phycoerythrin and the second preferentially exciting chl *a* (Fig. 79). A rough fluorescence emission spectrum can be recorded in 40 channels, each 11 nm wide, which routinely resolves distinct chl *a* (685 nm) and phycoerythrin, PE, (580 nm) fluorescence peaks whose relative intensities can be used to map the abundance of distinct groups of phytoplankton. (cf. Yentsch and Yentsch, 1984) Hoge and Swift (1983) used LIDAR dual laser excitation to map chl *a* and PE in a Gulf Stream Warm Core Ring, showing a wide spatial variation in the distribution of the two pigments that could be linked to transition zones between coastal, Gulf Stream and Sargasso Sea water masses. As more excitation wavelengths are employed and the resolution of the fluorosensor of LIDAR is improved, it should be possible to generate fluorescence emission spectra whose components can be further identified and to generate fluorescence excitation spectra to determine the major photosynthetic light-harvesting components. Combined with the absorption data from remote-sensing satellites and ground-truth data to keep the airborne instruments calibrated, it might be possible to estimate the relative fluorescence yield of photosynthesis (fluorescence/absorption) over wide areas and provide insights on the environmental factors regulating photosynthetic efficiencies in surface waters of the world's oceans. (p 449)

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158. Prezelin, B.B., R.R. Bidigare, M. Putt, B. Ver Hoven, *Diurnal patterns of size-fractionated primary productivity across a coastal front*. Mar. Biol., 1987. 96(4): p. 563-574.

In July 1985, diurnal patterns of photosynthesis and pigmentation were characterized for whole water ( $>0.4$   $\mu\text{m}$ ) and size-fractionated ( $>5$   $\mu\text{m}$  and 0.4 to 5  $\mu\text{m}$ ) communities from three light depths sampled across a coastal thermal front in the Southern California



Bight. Samples were collected predawn and held for 20 h in deck incubators. Variations in chlorophyll *a* and accessory pigment-to-chlorophyll *a* ratios showed no obvious diurnal trends. Timing of peak photosynthetic potential ( $P_{max}$ ) and its coincidence with variations in light-limited rates of photosynthesis ( $\alpha$ ) as well as diurnal amplitudes in  $P_{max}$  and  $\alpha$ , often differed between size fractions sampled within the same community. The same was true for identical size fractions collected from different depths and stations transecting the front. Primary productivity was 20-fold greater on the cold water side, where  $>5\ \mu\text{m}$  diatoms dominated the mixed layer and accounted for 80% of daytime productivity. Diatoms collected from the top and bottom of the upper mixed layer displayed nearly identical diurnal patterns in  $P_{max}$  and  $\alpha$ , with midday peaks exceeding predawn values by four-fold and two-fold respectively. Above the pycnocline, the 0.4 to 5  $\mu\text{m}$  fraction had lower assimilation rates than the  $>5\ \mu\text{m}$  fraction and smaller diurnal amplitudes in  $P_{max}$  and/or  $\alpha$ , with daytime patterns often characterized by two peaks interspersed by a short period of photoinhibition. Within the front, the 0.4 to 5  $\mu\text{m}$  fraction accounted for two-thirds of plant biomass and  $>90\%$  of primary production. Pigment analyses by high-performance liquid chromatography revealed enrichment in 19'-hexanoylfucoxanthin, indicative of enhanced numbers of prymnesiophytes. Photosynthetic activity in confined surface communities was susceptible to daytime photoinhibition, but subsurface communities exhibited midday  $P_{max}$  peaks that were three- to seven-fold predawn values. In the warm-water mass, both algal size fractions contributed equally to photosynthesis and chlorophyll *a* in surface waters, with the 0.4 to 5  $\mu\text{m}$  fraction becoming dominant at the base of the euphotic zone. At all depths, peak  $P_{max}$  of the 0.4 to 5  $\mu\text{m}$  fraction occurred before noon, while  $P_{max}$  of the  $>5\ \mu\text{m}$  fraction was clearly evident in the afternoon. Elevated chlorophyll *b*, 19'-hexanoylfucoxanthin- and zeaxanthin-to-chlorophyll *a* ratios indicated a mixture of algal groups, including chlorophytes, cyanobacteria and prymnesiophytes.

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159. Prezelin, B.B., H.E. Glover, and L. Campbell, *Effects of light intensity and nutrient availability on diel patterns of cell metabolism and growth in populations of Synechococcus spp.* Mar. Biol., 1987. 95(3): p. 469-480.

Between July 21 and August 8, 1984, phytoplankton were collected from the surface (2 m) and/or chlorophyll maximum of a neritic front, warm-core eddy 84-E and Wilkinson's Basin in the Northwest Atlantic Ocean and incubated up to 38 h in 200-liter vats. Effects of light intensity and nutrient availability on diel patterns of cell metabolism were analyzed in a 0.6- to 1- $\mu\text{m}$  fraction, where *Synechococcus* spp. represented 80 to 100% of the total photoautotrophs. Populations held under *in situ* conditions exhibited daytime peaks in photosynthetic potential ( $P_{max}$ ) that were an order of magnitude higher than nighttime  $P_{max}$  values. Daytime phasing of  $P_{max}$  peaks had no relationship to asynchronous fluctuations in cellular activities of ribulose 1,5 biphosphate carboxylase (RUPBCase), or to variations in chlorophyll content. Daytime  $P_{max}$  peaks were about 12 h out of phase with nighttime maxima in the frequency of dividing cells (FDC). The phase relationship between  $P_{max}$  and FDC could be altered by manipulating environmental conditions. High light exposure of deep populations did not affect timing of the  $P_{max}$  peak, but its magnitude increased and coincided with increased RUPBCase activity and chlorophyll photobleaching. In the eddy population, a major shift in the timing of peak  $P_{max}$  was induced when increased light intensity was accompanied by nutrient enrichment. This change coincided with major increases in cellular chlorophyll and carboxylating enzyme activity. Lowering irradiance and/or increasing nutrient availability elicited different diel patterns in cellular metabolism in surface populations from the eddy and from Wilkinson's Basin that appeared linked to differences in the nutrient

status of the cells. Rates of cell division estimated from the percentage of dividing cells in preserved samples were 0.83 divisions per day in surface warm-core eddy populations, supporting the view that carbon and nitrogen turnover rates in oligotrophic waters can be sufficient to promote near optimal growth of *Synechococcus* spp.

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160. Prezelin, B.B., H.E. Glover, B. Ver Hoven, D. Steinberg, H.A. Matlick, O. Schofield, N. Nelson, M. Wyman, and L. Campbell, *Blue-green light effects on light-limited rates of photosynthesis: Relationship to pigmentation and productivity estimates for Synechococcus populations from the Sargasso Sea*. Mar. Ecol. (Prog. Ser.), 1989. 54(1-2): p. 121-136.

It appears that *Synechococcus* populations are responsible for the majority of water column productivity in the open sea. They often are order of magnitude more abundant in the upper euphotic layer of the mid-Atlantic than all size categories of Chl-fluorescing cells combined. The phycoerythrin (PE) maximum lies above the chlorophyll maximum. (Table I) The impact of blue-green light incubation on short-term diurnal, daily, and integrated water column estimates of whole water ( $>0.2 \mu\text{m}$ ) and *Synechococcus*-specific photosynthesis was assessed throughout the euphotic zone at 2 stations in the Sargasso Sea. Replicate samples were incubated under both tungsten white light and broad band blue-green light, where the latter simulated light quality within the upper water column of the open sea. Diurnal variations in size-fractioned blue-green vs. white light photosynthesis-irradiance curves, chlorophyll and PE concentrations, and cell abundance of PE-rich cyanobacterial *Synechococcus* spp. and Chl-fluorescing algae, were measured within samples from the surface, PE maximum, Chl maximum, and the base of the euphotic zone. *Synechococcus* spp dominated ultraphytoplankton communities down to the light depths of the PE maximum (3 to 7% surface illumination,  $I_0$ ) with maxima in cell abundance routinely located at light depths  $>50\%$   $I_0$ . Blue-green and white light incubation conditions generally did not affect light-saturated rates of photosynthesis ( $P_{\text{max}}$ ) but blue-green light routinely did provide much higher estimates of light-limited rates of photosynthesis. For size-fractioned subpopulations dominated by *Synechococcus* spp., blue-green light values of  $\alpha$  were  $>5$ -fold greater than white light estimates. Compared to white light estimates, blue-green light estimates of total daily integrated water column primary productivity were 6 to 13% higher, while the contribution of *Synechococcus* to overall primary productivity rose from between 57 and 61% to between 73 and 84%. From the surface down to about 5%  $I_0$ , the PE content of *Synechococcus* cells increased with decreasing light and/or increasing inorganic nitrogen availability. Increases in *Synechococcus* PE/cell occurred in direct proportion to blue-green light measurements of photosynthetic quantum efficiency, further indicating that these cyanobacteria are physiologically well suited to harvest photosynthetically utilizable light throughout a large portion of the euphotic zone.

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161. Putnam, E.S., ed. *System Concept for Wide-Field-of-View Observations of Ocean Phenomena from Space*. 1987, NASA, Earth Science and Applications Division, Washington, DC.

Satellite-acquired ocean-color data and sea-surface-temperature data are powerful tools for understanding biological and physical processes in the ocean on a global scale. From 1978 to 1986, the Coastal Zone Color Scanner (CZCS) aboard the Nimbus-7 satellite provided the first ocean color data. During this period researchers demonstrated that these data can be used to determine the abundance of ocean biota. As a result, many commercial, operational, and research applications were developed that take advantage of the direct relationship of the ocean's color to its phytoplankton content. Also, data from the

long-wavelength infrared bands of the Advanced Very High Resolution Radiometer (AVHRR) aboard the NOAA series of satellites have proven useful in developing global maps of sea-surface temperature. Used jointly, these data have given new insights into the role of the oceans in our biosphere as well as providing economic benefits to several major industries. This work demonstrates the need for an operational spaceborne sensor that would provide data on ocean color and sea-surface temperature simultaneously. Since the CZCS has become non-operational, this need has become acute. Recognizing the importance of satisfying this need and the opportunity for incorporating such a sensor on the Landsat-6 spacecraft, NASA Headquarters and EOSAT convened a Sea-viewing, Wide-Field-of-View Sensor (SeaWiFS) Working Group in early 1987 to: a) discuss and document commercial, operational, and research applications for wide-field-of-view ocean-color imagery from the Landsat-6 satellite, b) define users' requirements for sensor performance and for data products and dissemination, and c) determine the feasibility of meeting the users requirements with respect to sensor design, accommodation of the sensor on the Landsat-6 satellite, data collection and distribution, and necessary spacecraft and ground-station interfaces. The Working Group was organized into three panels, representing commercial and operational users of oceanographic data, research users, and those responsible for implementing the system. The Commercial and Operational Users' Panel identified two principal user groups. The first comprises the 36,000 - 37,000 ocean-going vessels engaged worldwide in fishing and marine transportation and U.S. Navy vessels. The second, smaller user group comprises the value-added and offshore oil and gas exploration and development industries. Ships at sea need the ocean-color data to locate fish populations, thereby improving catch efficiency, and to optimize ship routes, thereby reducing costs. Oil and gas exploration and development industries need the data to a) provide an accurate and detailed understanding of the oceanographic environment for offshore platform design, reducing the risks attendant to under-design, b) determine "weather windows" when offshore operations, such as shipping supplies, pipelaying, and platform installation, can be conducted most safely and efficiently, and c) provide timely information on strong current jets and eddies, since these can cause a loss of drilling time due to increased loads on the drilling riser. The value-added industry needs ocean-color data to support all of the above applications in providing interpreted data products to its clients. The Research Panel documented a number of important research goals that could be reached only through continued availability of ocean-color data. These goals are to a) specify quantitatively the ocean's role in the global carbon cycle and other biogeochemical cycles, b) determine the magnitude and variability of annual primary production by marine phytoplankton on a global scale, c) understand the fate of fluvial nutrients and the possible effect on carbon budgets, d) elucidate the coupling mechanism between upwelling and large-scale patterns in ocean basins, e) answer questions concerning the large-scale distributions and timing of spring blooms in the global ocean, f) acquire a better understanding of the processes associated with mixing along the edge of eddies, coastal currents, western boundary currents, etc., and g) acquire global data on marine optical properties.

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162. Reese, C., L.L. Richardson, F.P. Chavez, K.R. Buck, and T. Bates. *Phytoplankton population assessment by measurement of in situ spectral reflectance and accessory pigments*. in *Aquatic Sciences Meeting*. Am. Soc. Limnol. Oceanog. 1992. Santa Fe, NM.

Measurements of surface reflectance of the North Pacific were made during an April 1991 Pacific Sulfur Stratus Investigation (PSI) cruise. Spectral data acquisition was supported by water sampling (surface and CTD). Spectroradiometer data (370 to 950 nm at 2 nm resolution) were calibrated, and compared with phytoplankton counts and the results of photosynthetic and photoprotective pigment analysis by reverse-phase HPLC. Spectra were also analyzed in terms of *in situ* dimethylsulfide (DMS) production. Our objective is to

scale-up from surface reflectance measurements to satellite remote sensing of DMS producing phytoplankton blooms.

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163. Reid, F.M.H., E. Stewart, R.W. Eppley, and D. Goodman, *Spatial distribution of phytoplankton species in chlorophyll maximum layers off southern California*. Limnol. Oceanogr., 1978. 23(2): p. 219-226.

The phytoplankton species assemblages of the chlorophyll maximum layer and the surface layers were compared in March 1976 at several stations off southern California. The assemblages in the two layers were quite different in the southern inshore part of the study area but were similar offshore and in Santa Monica Bay to the north. In both layers the assemblages changed more abruptly offshore than alongshore and gave the impression of elongate bands of phytoplankton oriented parallel to shore. Principal component analysis resolved two axes which accounted for the preponderance of the variability of species abundances. Component I consisted of several dinoflagellate and one coccolithophorid species, component II of several diatom species and the pigmented ciliate *Mesodinium rubrum*.

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164. Richardson, L.L., *Optical properties of naturally occurring populations of algae and photosynthetic bacteria*. Eos, 1990. 71(2): p. 109.

Spectral reflectance signatures of a wide range of populations of algae and photosynthetic bacteria present in hypersaline ponds in Guerrero Negro, Mexico, were measured using a field spectroradiometer. Data were analyzed in two ways: 1) spectra from 370 to 950 nm were analyzed in terms of photosynthetic pigment composition, and related to the pigment complement of the different taxonomic groups. Signals due to light absorbance by chlorophylls *a* and *b*, carotenoids, phycobilins, bacteriochlorophylls, and bacteriorubins were distinctly evident. 2) Spectra were also analyzed in terms of studying population heterogeneity, both at one spatial scale and spanning different spatial resolutions. Spectra were taken in a grid pattern at resolutions from every 100 microns to every 30 m. To study population heterogeneity reflectance at 620 nm (the specific absorbance peak of the cyanobacterial pigment phycocyanin) were pulled from each spectrum at each scale and plotted 3-dimensionally against distance (reflectance vs. X & Y spatial distance) Data portrayed in this manner agreed with the spatial distribution of cyanobacteria in the mixed populations, both at the smallest scale investigated, and at 30 m spatial resolution. The latter agreed with digital data from a Landsat Thematic Mapper satellite image of the study area. We have combined our spectroradiometer and satellite data with results from *in situ* geochemical experiments on inorganic and organic carbon flux in two pond systems (one dominated by diatoms, the other by cyanobacteria) to obtain estimates of ecosystem-wide flux. Our results are significant in terms of potential use of optical data to study population dynamics and ecosystem level biogeochemical cycling.

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165. Richardson, L.L., D. Bachoon, V. Ingram-Willey, C.C. Chow, and K. Weinstock, *Remote sensing of the biological dynamics of large-scale salt evaporation ponds*. In Proceedings, 24th International Symposium on Remote Sensing of Environment, 1991. Rio de Janeiro, Brazil. 2: p. 611-623.

Optical properties of salt evaporation ponds associated with Exportada de Sal, a salt production company in Baja California Sur, Mexico, were analyzed using a combination of spectroradiometer and extracted pigment data, and Landsat-5 Thematic Mapper imagery. The optical characteristics of each pond are determined by the biota, which consists of dense populations of algae and photosynthetic bacteria containing a wide variety of photosynthetic and photoprotective pigments. Analysis has shown that spectral and image data can differentiate between taxonomic groups of the microbiota, detect changes in population distributions, and reveal large-scale seasonal dynamics.

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166. Riemann, B., *Carotenoid interference in the spectrophotometric determination of chlorophyll degradation products from natural populations of phytoplankton*. *Limnol. Oceanogr.*, 1978. 23(5): p. 1059-1066.

Pigments extracted from natural populations of diatoms showed increased absorption between 600-750 nm after acidification with HCl at concentrations above  $3 \times 10^{-3}$  M, both in 90% acetone and absolute methanol. This increase in absorption, due to spectral changes in fucoxanthin, made reliable spectrophotometric distinction between chlorophyll *a* and pheopigments impossible. Changes in absorption spectra of chlorophyll *a*, pheophytin *a*, diatoxanthin, and carotene were of minor importance. Corrections for chlorophyll degradation products should be made with care to ensure that the presence of pheopigment *a* is legitimate and not a function of the ratios of epoxidic carotenoids to chlorophyll *a*.

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167. Robinson, I.S., *Satellite Oceanography: An Introduction for Oceanographers and Remote-Sensing Scientists*. Ellis Horwood Series in Marine Science, ed. T.D. Allan. 1985, Chichester: Ellis Horwood Limited (Halsted Press). 455 p.

Book for practising oceanographers, for sensor technologists and remote-sensing specialists, and for graduate and undergraduate students of both oceanography and remote sensing. Table of Contents: Chap.1 Oceanography from space? *Section A* Chap.2 The possibilities in space - space hardware and data transmission. Chap. 3 The possibilities for oceanography. Chap. 4 Principles of remote sensing of the sea. Chap. 5 Principles of image processing. *Section B* Chap. 6 Visible wavelength 'ocean color' sensors. Chap. 7. Sea-surface temperature from infrared scanning radiometers. Chap. 8 Passive microwave radiometers. Chap. 9 Satellite altimetry of sea-surface topography. Chap. 10 Active microwave sensing of sea-surface roughness. Chap. 11 The altimeter as a surface-roughness sensor. Chap. 12 Synthetic aperture radar. Chap. 13 Microwave scatterometers. Chap. 14 The way forward. Of greatest interest here is the last chapter: "The one area of ocean colour research where there remains a need for a technological breakthrough is in fluorometry. The laser fluorometer promises to be a powerful remote-sensing tool for marine biologists, chemists, and physicists, but at present it is difficult to envisage it being flown on anything higher than an aircraft."

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168. Sakshaug, E., G. Johnsen, O. Samseth, and Z. Volant, *Identification of phytoplankton blooms by means of remote sensing*. in *Environment Northern Seas*. 1991. p. 91-100.

By using a 3-wavelength band (blue, green and red) light beam attenuation meter suspended from a buoy, it is possible to distinguish between main groups of bloom-forming phytoplankton, for instance toxic prymnesiophytes and dinoflagellates vs non-toxic diatoms.

Measurements at additional wavelengths make it in principle also possible to distinguish between ecologically important algae at the species level. If, however, information gathering is to be optimized, a multi-wavelength instrument should incorporate sensors for the measurement of light beam attenuation in combination with sensors for the measurement of chlorophyll fluorescence at corresponding excitation wavelengths. The advantages of this approach are discussed. The ideal investigation in the context of in-depth studies of phytoplankton ecology is therefore one which includes both remote sensing and the deployment of ships, with additional support from laboratory experiments. Although a phytoplankton bloom is usually dominated by one or, at maximum three species, species composition will differ from one bloom to another. About 300 different algal pigments have been identified, and the optical properties of algae differ from species to species because the pigment composition differs. In the marine environment of the north, the main pigments which may be used to distinguish between species are three forms of Chlorophyll *c* and the carotenoids. The three predominant groups are diatoms, dinoflagellates and prymnesiophytes. The dinoflagellate pigment composition is closely related to brown seaweeds, and the most important carotenoid is fucoxanthin (520-530 nm) along with Chlorophyll *c1* and *c2*. Prymnesiophytes can form blooms of toxic species which are harmful to fish and bottom fauna. Another species (*Phaeocystis pouchetii*) is non-toxic, but can drift ashore in huge quantities where they form a foamy and stinking mass. Toxic prymnesiophytes have in addition to fucoxanthin the carotenoid 19'hexanoyloxy-fucoxanthin, which causes a distinct shoulder in the spectrum at 470 nm, and Chlorophyll *c3*. There is also a non-toxic group of prymnesiophytes called coccolithophorids which are in principle easily identifiable by remote sensing because they, in contrast with other algae, backscatter considerable amounts of light at all wavelengths. The majority of dinoflagellates have the mahogany-red carotenoid peridinin as the major carotenoid, while a few, among them some globally distributed toxic species have 19'hexanoyloxy-fucoxanthin and chlorophyll *c3*, like some prymnesiophytes. Toxic dinoflagellates can cause shellfish toxicity or mass mortality of fish. Optical identification of algal species depends both on how different the absorption spectra of different species are, and at how many wavelengths one can do measurements. A "Zsolmeter" is a telemetric beam attenuation meter which can be suspended from buoys, and which can deliver readings of ratios between any two of three wavelengths: 470 nm, 560 nm and 660 nm. Laboratory cultures of a prymnesiophyte gave higher B/R and B/G readings than those for a diatom. However, the differences for field populations were smaller because the natural populations are not unialgal, but still significant. In order to assess the possibility of "optical systematics", discriminant analysis was performed on the light absorption spectra of cultures of several algal species. (Fig.4) The various groups with contrasting pigmentation are spread out on such a graph. There is a clear separation between toxic prymnesiophytes and dinoflagellates on one hand and non-toxic diatoms on the other. Fluorescent excitation spectra for the emission at 684 nm identify only phytoplankton (no interference from dead particles or non-algal microorganisms). Since fluorescence arises only from photosystem II, it does not respond to absorption by photoprotective pigments. And fluorescence excitation spectra exhibit more detailed and distinct patterns than light absorption spectra as a function of variations in carotenoid, chlorophyll, and biliprotein contents of the cells, which implies that algal species may be easier to identify on the basis of fluorescence spectra than light absorption spectra. The future without doubt will belong to technologies which incorporate sensors for measurements of both the beam attenuation of light and chlorophyll fluorescence; no more than 4-6 different wavelengths may be sufficient.

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169. Saltzman, B. (editor). *Satellite Oceanic Remote Sensing*. 1985. Advances in Geophysics, 27. Orlando, Academic Press

There are 11 chapters and 5 appendices, of which only Chap. 8 (Ocean Color Measurements by H.R. Gordon, R.W. Austin, D.K. Clark, W.A. Hovis, and C.S. Yentsch) is of interest for this review. The emphasis is almost entirely on the CZCS and detection of chlorophyll *a*. It is, however, an excellent overview.

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170. Sathyendranath, S. *Remote sensing of phytoplankton: A review, with special reference to picoplankton*. Can. Bull. Fish. Aquatic Sci., 1986. 214: p. 561-583

This review addresses two questions: How do picoplankton affect the remotely sensed signal? Can remote sensing tell us anything about picoplankton? In the absence of information on the effects of picoplankton, efforts to evaluate their implications for remote sensing will have to be based entirely on information available from theoretical, laboratory and *in situ* studies. The paper has three sections: first the signal leaving the water surface is derived from the signal received by a sensor on a remote platform; next, the diverse techniques of phytoplankton remote sensing (passive radiometry, passive fluorescence, and active lidar techniques) are examined; finally, the limitations of the depths accessible by remote sensing are studied. The summary and conclusions are as follows: where passive radiometric techniques based on changes in ocean color are concerned, there seems to be no doubt that the picoplankton will leave their imprint on the water-leaving radiance, which serves as a signal for remote sensing. Their small size favors higher specific absorption, and so their effect on the signal may be more important than warranted by considerations of the concentrations alone. The absorption spectra of these blue-green algae (cyanobacteria) are very distinct from other types of phytoplankton. Since the relative abundance of picoplankton appears to be higher in oligotrophic waters, a suitable method is needed that can monitor small changes in their concentration on a synoptic scale; passive radiometric methods seem to be suitable for such applications. The possibility of employing variations in spectral signatures of different types of phytoplankton to separate the signals from various taxonomic groups of phytoplankton remains to be explored, as it would require working with much higher spectral and radiometric resolution than is currently available. Active fluorescence techniques have demonstrated the capability of picking up the phycoerythrin fluorescence signal, making it possible to monitor a blue-green fraction of the picoplankton at least, if not all the picoplankton. However, investigators must rely on alternate supporting data to ensure that the phycoerythrin is in fact in the picoplankton, and not in larger cyanobacteria such as *Oscillatoria* (*Trichodesmium*) or even cryptomonads or rhodophytes. Ocean color techniques, and emerging active and passive fluorescence techniques do not yield redundant information. By combining the methods suitably, it is becoming possible to obtain more accurate estimates, particularly for primary productivity. Fluorescence techniques may be best suited for monitoring areas of high phytoplankton concentration, while ocean color is more sensitive at lower pigment concentration. The depth of the water column sampled by the two techniques differs significantly, which could be used for deriving information on the vertical distribution of pigments. There appears to be no optical method at present which would allow us to derive information on the size distribution of suspended material by remote sensing.

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171. Sathyendranath, S. and T. Platt, *The spectral irradiance field at the surface and in the interior of the ocean - A model for applications in oceanography and remote sensing*. J. Geophys. Res., 1988. 93(Aug.15): p. 9270-9280.

A spectral model of irradiance is presented for the computation of light energy available at the surface and at various depths in the ocean for the wavelength range from

400 to 700 nm. For any latitude, irradiances are computed as a function of geographic location, date, and time. Application of the model is demonstrated through computation of the profiles of vertical attenuation coefficient and of the effective specific absorption of phytoplankton. The model results are compared with those from conventional procedures, which disregard spectral and angular distributions of the underwater light field, for calculation of the effective specific absorption. The magnitude of the errors incurred by such simplifications is estimated and is shown to be non-negligible and variable with solar elevation, depth, and the phytoplankton pigment concentration in the water.

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172. Sathyendranath, S. and T. Platt, *Remote sensing of ocean chlorophyll - consequence of nonuniform pigment profile*. Applied Optics, 1989. 28(Feb. 1): p. 490-495.

Remote sensing of ocean color, applied to the estimation of chlorophyll (Ch) biomass is discussed for the case where the vertical phytoplankton pigment profile (PP) is nonuniform. Using a spectral model of reflectance, the consequences of vertical structure are evaluated by sensitivity analysis on a generalized PP. It is shown that the assumption of a vertically homogeneous Ch distribution can lead to significant errors (relative error exceeding 100 percent) in the estimation from satellite data of photic depth and total pigment content in the photic zone. The errors are shown to be functions of the parameters of the PP. It is further shown that, if the shape of the PP is known from independent data, the entire PP may be recovered from the satellite data by making slight changes in the existing algorithms for Ch retrieval.

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173. Sathyendranath, S., A.D. Gouveia, S.R. Shetye, P. Ravindran, and T. Platt, *Biological control of surface temperature in the Arabian Sea*. Nature, 1991. 349(Jan.3): p. 54-56.

By far the dominant variable parameter controlling the absorption cross-section for short-wavelength solar radiation incident on the ocean surface is the concentration of photosynthetic pigment contained in phytoplankton cells. The abundance of phytoplankton depends on the intensity of incident radiation and on the supply of essential nutrients (nitrogen in particular). A higher abundance increases absorption of radiation and thus enhances the rate of heating at the ocean surface. In the Arabian Sea, the southwest monsoon promotes seasonal upwelling of deep water, which supplies nutrients to the surface layer and leads to a marked increase in phytoplankton growth. Remotely sensed data on ocean color are used here to show that the resulting distribution of phytoplankton exerts a controlling influence on the seasonal evolution of sea surface temperature. This results in a corresponding modification of ocean-atmosphere heat exchange on regional and seasonal scales. It is shown that this biological mechanism may provide an important regulating influence on ocean-atmosphere interactions.

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174. Schofield, O., R.R. Bidigare, and B. Prezelin, *Spectral photosynthesis, quantum yield and blue-green light enhancement of productivity rates in the diatom Chaetoceros gracile and the prymnesiophyte Emiliana huxleyi*. Mar. Ecol. (Prog. Ser.), 1990. 64: p. 175-186.

The photosynthetic properties of white and blue-green light grown cultures of a diatom, *Chaetoceros gracile*, and a prymnesiophyte, *Emiliana huxleyi*, were compared. The aim of the study was to quantify chromaticity effects on the spectral properties of chromophytes which significantly impact bio-optical predictions of *in situ* primary production. The



comparisons emphasized the spectral dependency of cell pigmentation, absorption, quantum yield and rates of photosynthesis. Concentrations of chlorophylls and carotenoids were similar for the white light cultures of *C. gracile* and *E. huxleyi*. While the absorption spectra for the chromophytes were similar, *E. huxleyi* exhibited a higher quantum efficiency and hence a higher photosynthetic rate, than *C. gracile*. The pattern of blue-green light adaptation was quite distinct for the 2 phytoplankters. The diatom exhibited little change in pigmentation, but relative quantum yield increased slightly as did overall rates of photosynthesis. In the prymnesiophyte, total cell pigmentation was reduced by half, lowering cell absorption while increasing *in situ* chlorophyll-specific rates of photosynthesis. Carbon action spectra were made with and without background blue-green light in order to assess the potential errors produced by restricted 'Emerson enhancement effects' which are inherent in the measurement of photosynthetic action spectra. Rates of photosynthesis increased 17 to 36% when enhancement effects were taken into account. These direct measures of photosynthesis were in good agreement with bio-optical model predictions based on the spectral properties of chromophytes.

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175. Schofield, O. and B.B. Prezelin. *Analysis of the variability in the maximum and the operational quantum yield in the Southern California Bight (SCB)*. in *Aquatic Sciences Meeting*. Am. Soc. Limnol. Oceanog. 1992. Santa Fe, NM.

The spatial and temporal variability in maximum and operational quantum yield was determined for diverse algal assemblages sampled over 200 km of the SCB and over time within the Southern California Counter Current (SCCC). To determine which hydrographic and biological variables described the observed variability in quantum yield, multiple linear regressions were conducted for the entire or subsetted databases (i.e. SCB, SCCC). Backward stepwise regression was used to delineate the most significant independent variables (pigments,  $Q_{par}$ ,  $NO_3$ , sigma-t, etc.) for the regression of quantum yield. Regression analyses of variability in  $P_{max}$  &  $I_k$ , the major photophysiological components of quantum yield, were carried out in an identical manner. Results will be discussed in the context of their implications for the modeling of quantum yield.

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176. Shapiro, L.P., E.M. Haugen, M.D. Keller, R.R. Bidigare, L. Campbell, and R.R.L. Guillard, *Taxonomic affinities of marine coccoid ultraphytoplankton: A comparison of immunochemical surface antigen cross-reactions and HPLC chloroplast pigment signatures*. J. Phycol., 1989. 25(4): p. 794-797.

The phytoplankton assemblage of most marine environments, at least seasonally, is dominated by minute coccoid and flagellated cells. Cells of these clones have few distinguishing morphological features which can be resolved with the light or electron microscope. Immunological grouping, determined by affinities of polyclonal antibodies to surface antigens of intact cells, was used to characterize 19 clones of marine coccoid ultraplankton. The resulting cross-reactive antigen groups corresponded to pigment-groups as defined by HPLC analysis of chloroplast pigments (carotenoids and chlorophylls). Because immunological cross reactions are specific at the species level in groups of algae having well defined morphological criteria, we suggest that immunological methods can be used to recognize algae presently indistinguishable by standard morphological criteria, and especially in oceanographic applications involving qualitative cell enumerations of the ultraplankton.

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177. Shapiro, L.P., E.M. Haugen, and E.J. Carpenter, *Occurrence and abundance of green-fluorescing dinoflagellates in surface waters of the northwest Atlantic and northeast Pacific oceans*. J. Phycol., 1989. 25: p. 118-120.

We have cultured green fluorescing heterotrophic dinoflagellates whose continuous green fluorescence is due to an unidentified compound, probably a flavin, that excites with blue light and emits green light. No evidence of bioluminescence was found, but we note that compounds with similar fluorescence characteristics have been associated with bioluminescence in other taxa. These cells, all naked gymnodinoids, are widespread and abundant in the Northwest Atlantic and Northeast Pacific Oceans. They comprise 4-100% of the total heterotrophic dinoflagellate component which, in turn, is usually equivalent in magnitude to the phototrophic naked dinoflagellate component of the phytoplankton community.  
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178. Shapiro, D.B., M.S. Quinby-Hunt, and A.J. Hunt. *Origin of the induced circular polarization in the light scattering from a dinoflagellate*. in *Ocean Optics X*. 1990. Orlando, FL 1302: p. 281-289.

The S<sub>11</sub> and S<sub>14</sub> scattering matrix elements were measured for light scattered from single dinoflagellates and single irregularly-shaped alumina particles suspended in a transparent gel. The S<sub>14</sub> matrix element indicates the degree of circularly-polarized light induced on incident unpolarized light. The S<sub>14</sub> signal from the dinoflagellates was found to be significantly larger than that measured for the alumina particles. The nucleus of the dinoflagellate investigated, *Prorocentrum micans*, contains about 50 structurally complex chromosomes with a helical structure. This work provides evidence in support of the hypothesis that the observed S<sub>14</sub> signal produced by the light scattering from *P. micans* is due to the helical nature of the chromosomes.  
Applied Science Division, Lawrence Berkeley Laboratory, University of California, Berkeley, CA 94720

179. Siegel, D.A., R. Iturriaga, R.R. Bidigare, R.C. Smith, H. Pak, T.D. Dickey, J. Marra, and K.S. Baker, *Meridional variations of the springtime phytoplankton community in the Sargasso Sea*. J. Marine Research, 1990, 48: p. 379-412.

Meridional distributions of particle, pigment, optical, chemical and physical *in situ* oceanographic properties, as well as satellite-sensed sea-surface temperature and color imagery, are used to investigate phytoplankton community distributions and their relation to the near-surface water masses of the Sargasso Sea. Measurements were made during April of 1985 along a 1200 km transect on 70° W (from 24° N to 35° N). The seasonal evolution of subtropical Mode water (18° C water) is shown to be the primary factor controlling the spatial distribution and evolution of the phytoplankton community in the northern Sargasso Sea (31° to 35° N). The springtime near-surface restratification of recently ventilated 18° C water initiated a diatom-dominated phytoplankton bloom. As the bloom declined, the phytoplankton community evolved into a diverse assemblage. The consequences of these phytoplankton successions were observed both temporally and as spatial variations. Seasonal depletions of ozone in the Antarctic austral spring have already reached 50%. Since UV-B radiation can penetrate to ecologically significant depths in water, any ozone reduction results in increased UV-B penetrating the surface layers of marine environments. Action spectra correspond to either protein or nucleic acids. A 25% depletion of stratospheric ozone --> 9% decrease in marine primary productivity. Studies suggest that natural communities would show alteration of algal community structure as this region.  
Woods Hole Oceanographic Institution, Woods Hole, MA 02543

180. Smith, R.C. and K.S. Baker, *The bio-optical state of ocean waters and remote sensing*. Limnol. Oceanogr., 1978. 23(2): p. 247-259.

The diffuse attenuation coefficient for irradiance,  $K_t$ , is a physical measure of the bio-optical state of ocean waters. From an analysis of irradiance,  $K_t$ , and pigment concentration, the specific attenuation due to chlorophyll-like pigments is found to be  $0.016 \pm 0.003$  [ $\text{m}^{-1}(\text{mg pigment m}^{-3})^{-1}$ ]. The bio-optical state of ocean waters can be remotely sensed by spacecraft sensors.  $K_t$  is readily measured at sea and is highly correlated with and dependent on the chlorophyll-like pigment concentration,  $C_K$ . This pigment concentration and  $K_t$  provide a measure of the fraction of radiant energy attenuated by phytoplankton. This fraction, in turn, is closely related to the production equations formulated by Bannister and can be directly incorporated into a general theory of phytoplankton dynamics.  $C_K$  may also be used as an index of primary productivity. The determination of the bio-optical state of ocean waters by surface vessels provides direct information concerning the productivity of these waters. To the extent that the bio-optical state can be determined by satellite, it may be possible to examine important parameters of the marine ecosystem rapidly and repeatedly.

Visibility Laboratory, Scripps Institution of Oceanography, University of California, San Diego, La Jolla 92093.

181. Smith, R.C. and K.S. Baker, *Optical classification of natural waters*. Limnol. Oceanogr., 1978. 23(2): p. 260-267.

A technique has been developed that leads to an optical classification of natural waters in terms of the dissolved and suspended biogenous material present. As a first approximation, this classification has been made in terms of the total chlorophyll-like pigment concentration. A relationship between the spectral diffuse attenuation coefficient for irradiance and the chlorophyll-like pigment concentration has been found with spectral irradiance data from diverse types of ocean waters. The specific spectral attenuation coefficient due to phytoplankton is shown to be consistent with laboratory measurements of the diffuse absorption coefficient of various lot cultures of phytoplankton.

Visibility Laboratory, Scripps Institution of Oceanography, University of California, San Diego, La Jolla 92093

182. Smith, R.C. and K.S. Baker, *Oceanic chlorophyll concentrations as determined by satellite (Nimbus-7 Coastal Zone Color Scanner)*. Mar. Biol., 1982. 66: p. 269-279.

Data gathered concurrently by ships and satellite (Nimbus-7 Coastal Zone Color Scanner) have been compared to optimize a general chlorophyll algorithm and to calculate chlorophyll concentrations in the Southern California Bight. This optimization provides regional images of chlorophyll concentration that are consistent with independent shipboard chlorophyll determination within  $\pm 40\%$ . Chlorophyll images from satellite passes on 27 February, 6 March and 11 March 1979 are presented along with shipboard measurements to reveal complex and changing chlorophyll patterns including a significant decline in the mean chlorophyll concentration during the 2 week study. These data provide a synoptic view of a complex oceanographic region which is impractical to obtain from ships alone. It is shown how concurrent ship and satellite data can be used for the quantitative definition and statistical analysis of an oceanic habitat descriptor (chlorophyll) for the modeling of the marine environment.

Bio-Optical Group, Dept. Biol. Sciences, Geography Dept. University of California, Santa Barbara CA 93106

183. Smith, R.C., R.R. Bidigare, B.B. Prezelin, K.S. Baker, and J.M. Brooks, *Optical characterization of primary productivity across a coastal front*. Mar. Biol., 1987. **96**(4): p. 575-591.

Methods for the remote estimation of phytoplankton biomass and production rates using multiplatform sampling strategies are essential for the better understanding of oceanic bio-geochemical cycles. Recent advances in remote sensing of ocean color have made synoptic estimation of phytoplankton biomass attainable. While considerable success has been achieved in the estimation of plant biomass, the synoptic estimation of phytoplankton rates of production has been inadequate. Rapid shipboard estimates of the vertical distribution of primary productivity, on mesoscale spatial scales and event-time scales, are needed to provide both surface validation and data for the development of bio-optical models linking production to the optical characteristics of the water column. This study details the primary productivity and optical properties of a frontal region in July 1985 along 35° 50' N in the Southern California Bight which is shown to be consistent with the concurrent high-performance liquid-chromatography pigment analysis. Authors describe here a "quasi-synoptic" shipboard bio-optical sampling strategy across a frontal region as an example of time-corrected data for assessing phytoplankton production in highly variable ocean regions. (Table I provides correlations of pigments with algal groups) **80 refs**

Bio-Optical Group, Dept. Biol. Sciences, Geography Dept. University of California, Santa Barbara CA 93106

184. Smith, R.C., X. Zhang, and J. Michaelson, *Variability of pigment biomass in the California Current system as determined by satellite imagery 1. Spatial variability*. J. of Geophysical Res., 1988. **93**(D9): p. 10,863-10,882.

Spatial variability of chlorophyll in the California Current system was analyzed using Coastal Zone Color Scanner imagery. A total of 48 images was analyzed to produce seasonal averages and variances, gradients, and power spectra. Roughly one third to one half of the variance in pigment biomass can be explained by consistent, large-scale gradients. In general, biomass is higher in the north and in nearshore areas. Nearshore areas also have proportionally more small-scale variability than the areas offshore. Slopes of the power spectra for nearshore areas are about -2.2 (for spatial scales of 10-100 km), while slopes for offshore areas are about -3. In addition, the power spectra show evidence of a change in slope at about 10 km, with slopes of ~-1 for shorter-length scales. This may indicate that biological processes dominate the smaller scales, while mesoscale eddies and geostrophic currents dominate the larger scales.

Center for Remote Sensing and Environmental Optics, Department of Geography, University of California, Santa Barbara, CA 93016

185. Smith, R.C. and K.S. Baker, *Stratospheric ozone, middle ultraviolet radiation and phytoplankton productivity*. Oceanography, 1989. (November): p. 4-10.

Marine life in the upper layers of the sea may be endangered by increased UV radiation, especially UV-B, resulting from reduction in the thickness of the earth's ozone layer. Seasonal depletions of ozone in the Antarctic austral spring have already reached 50%. Since UV-B radiation can penetrate to ecologically significant depths in water, any ozone reduction results in increased UV-B penetrating the surface layers of marine environments. Action spectra correspond to either protein or nucleic acids. A 25% depletion of stratospheric ozone -->9% decrease in marine primary productivity. Studies suggest that natural communities would show alteration of algal community structure as a result of exposure to enhanced levels of UV-B radiation. Direct influence of UV-B on protein content, dry weight, and pigment concentration have been demonstrated. It is difficult to extrapolate laboratory studies to predictions of possible impacts at the community and ecosystem level.

The extreme change in ozone association with a hole produces a sharp gradient which creates a UV-B front analogous to an oceanographic front. Comparative studies of UV-B effects across this front may provide a natural laboratory for direct observation of the impact of UV-B on natural phytoplankton communities. The need is great for direct measures of ultraviolet radiation effects on natural communities in the world's oceans.

Center for Remote Sensing and Environmental Optics, Department of Geography, University of California, Santa Barbara, CA 93016

186. Smith, R.C., B.B. Prezelin, R.R. Bidigare, and K.S. Baker, *Bio-optical modeling of photosynthetic production in coastal waters*. Limnol. Oceanogr., 1989. 34(8): p. 1524-1544.

A physiological-based bio-optical model is used to estimate vertical profiles of instantaneous, diurnal, and integrated daily rates of *in situ* primary production throughout the water column at three stations across a coastal front. The model makes use of an empirical relationship between photosynthesis, quantum yield, and photosynthetically absorbed radiation and is a full spectral model with all relevant parameters determined as a function of wavelength. In the prior application of this bio-optical model, parameters used to estimate quantum yield as a function of irradiance were wavelength-independent and held constant. Here, the model is recast so that quantum yield is estimated with wavelength-dependent photosynthesis-irradiance (P-I) parameters,  $P_{max}$  the maximum rate of phytoplankton photosynthesis, and  $I_k$ , the P-I saturation parameter are allowed to vary with depth and time of day. Both  $P_{max}$ -dependent (assumed to be wavelength-independent) and  $I_k$ -dependent (known to be wavelength-dependent) estimates of temporal/spatial changes in quantum yield were assessed. The model was tested in water masses where a net-to-nanoplankton transition was occurring in phytoplankton communities dominated by diatoms and prymnesiophytes. At each station there is close agreement between  $^{14}C$  productivity estimates derived from knowledge of diurnal patterns in P-I parameters and productivity estimates derived from two variants of the bio-optical model based on knowledge of spectral irradiance and phytoplankton pigmentation. The  $^{14}C$  and bio-optical estimates of photosynthetic rates give a closer match than bio-optical estimates that are  $P_{max}$ -dependent. The model permits calculation of primary production from shipboard observations and may be useful for predicting production rates from bio-optical data provided by untended buoys. CSL/Center for Remote Sensing and Environmental Optics, UCMBO and Geography Department, University of California at Santa Barbara, Santa Barbara, CA 93016

187. Stegman, P., *Solar-stimulated fluorescence and its implications for remote sensing*. Eos, 1987. 68: p. 1694.

Solar-stimulated fluorescence has been considered as a possible means by which to map synoptically phytoplankton pigment concentration and, more recently, primary productivity. Shipboard measurements of biological parameters and upwelling radiance were conducted to study this relationship. Results revealed a quite variable fluorescence intensity with no similar fluctuations observed in the biological parameters. An optical model was therefore developed to examine this variability. A thus derived fluorescence efficiency factor, which indicates the amount of fluorescence emitted per unit incident irradiance and chlorophyll concentration, remained (in 90% of the calculations) at a low level regardless of phytoplankton pigment concentrations. What meaning these consistently low values might have for remote sensing of phytoplankton biomass and primary productivity via passive fluorescence measurements is discussed.

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188. Stevenson, R.E., *Oceanography from the Space Shuttle*. 1989, University Corporation for Atmospheric Research and the Office of Naval Research, United States Navy.

Photographs from the space shuttle. Beautiful, but little of interest on ecology. One photograph (p131) is of a bloom of reddish-colored phytoplankton in the Red Sea, blown into a concentrated, broad, area. The Introduction states: "the human eye and brain, with the aid of optics, have the ability to observe oceanographic phenomena in the visual part of the electromagnetic spectrum over broader physical scales and between more subtle changes in color than any unmanned sensor technology currently being flown in space."

189. Stramski, D. and D.A. Kiefer. *Optical properties of marine bacteria*. in *Ocean Optics X*. 1990. Orlando, FL 1302: p. 250-268. SPIE.

Optical properties of naturally derived bacterioplankton grown in unenriched seawater are described. The beam attenuation coefficient, absorption coefficient and size distribution of cells in a suspension of bacteria were measured in order to determine their optical efficiency factors. In addition, the refractive index as well as the angular pattern of light scattering were obtained from Mie theory. The cellular scattering efficiency increases with decreasing light wavelength as  $\lambda^{-2}$ , the backscattering efficiency is almost spectrally neutral, and the absorption efficiency exhibits features associated with respiratory cytochromes. Except for backscattering, the efficiencies are significantly lower than those for larger biological microparticles. We suggest that bacteria are a major source of light scattering in oligotrophic waters, where their contribution to the scattering coefficient may far exceed 50%. This large contribution is caused by the fact that total geometric cross sectional area for the bacteria compensates for their lower scattering efficiency. The contribution by bacteria to particle absorption, although less certain, appears also to be important in oligotrophic waters, and it may even predominate a non-phytoplankton component. The effects of changes in size and refractive index on optical efficiencies of bacteria are also discussed in terms of a recent hypothesis concerning the regulation of cellular water content.

Dept. of Biological Sciences, University of Southern California, Los Angeles, California 90089-0371

190. Strong, A.E. and B.J. Eadie, *Satellite observations of calcium carbonate precipitations in the Great Lakes*. Limnol. Oceanogr., 1978. 23(5): p. 877-887.

Reflectance patterns apparently from calcium carbonate precipitation have been mapped in the Great Lakes using satellite multispectral imagery. The milky water phenomenon ("whiting") occurred regularly in summer and fall during the period studied, 1972-1975, in Lakes Ontario, Erie, and Michigan but not in Superior and Huron. *In situ* data provide nearly irrefutable evidence that these whittings are calcareous. They are attributed to supersaturation of  $\text{CaCO}_3$  during periods of thermal stratification and are most intense in the warmer areas of the lakes. The whittings are maximal several meters below the surface and are undoubtedly significant with respect to light transmission, affecting the euphotic zone and thereby photosynthetic production. They may serve as lakewide markers in synoptic analysis of large-scale epilimnial horizontal motions.

National Environmental Satellite Services, NOAA, Washington D.C. 20233, Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, Michigan 48104

191. Subramanian, A., P. Falkowski, D.G. Capone, E.J. Carpenter. *Does Trichodesmium facilitate "echo blooms" of phytoplankton?* in *Aquatic Sciences Meeting*. Am. Soc. Limnol. Oceanog. 1992. Santa Fe.

*Trichodesmium*, a marine nitrogen fixing cyanobacterium, commonly blooms in tropical oligotrophic oceans. Live and decaying *Trichodesmium* colonies collected in the Caribbean Sea exuded nitrogenous nutrients with release rates of up to  $0.02 \mu\text{M}/\text{hour}$  of

ammonium per colony. The potential for the nutrient enrichment caused by *Trichodesmium* blooms to contribute to the formation of "echo blooms" was explored using scenes from the Coastal Zone Color Scanner (CZCS). *Trichodesmium* blooms were identified and tracked in CZCS scenes from the Indian Ocean. The disappearance of a *Trichodesmium* bloom and the appearance of another phytoplanktonic bloom within a week can be seen in sequential scenes of the region. The importance of the "new" nitrogen introduced by *Trichodesmium* to "new" production will be discussed. In his talk, Subramanian asserted that *Trichodesmium* had a distinctive spectral signature. While the cells are microscopic, they occur in chains which coalesce into masses which are visible to the naked eye, and gas bubbles make them float. Thus the important question of nitrogen fixation and its effects in the ocean can be addressed. He uses band 3 (550 nm) and notes the chlorophyll associated with the phycoerythrin. He calculates 11 µgC/colony, and 2 µgN/colony. A bloom requires phosphorous, and is eaten by copepods.

MSRC, SUNY at Stony Brook, Stony Brook, NY 11794.

192. Sweeny, B.M., D.C. Fork, and K. Satoh, *Stimulation of bioluminescence in dinoflagellates by red light*. Photochem. Photobiol., 1983. 37(4): p. 457-465.

In three species of dinoflagellate, *Gonyaulax polyedra*, *Pyrocystis fusiformis* and *Pyrocystis lunula*, bioluminescence can be stimulated by light. This phenomenon is observed if the cell suspension is rendered anaerobic by any of the following treatments: N<sub>2</sub> gas, metabolically active yeast, glucose plus glucose oxidase, dithionite or allowing a concentrated cells suspension to stand for several hours in darkness, conditions which remove oxygen from the cell suspension. An alternate pretreatment is inclusion of carbonylcyanide-*m*-chlorophenyl hydrazone or hydroxylamine in the cell suspension. The action spectrum (maximum at 675 nm in the red region of the spectrum) points to chlorophyll as the photoreceptor. Evidence for the participation of photosystem II (PSII) of photosynthesis in the light-stimulation of bioluminescence is the strong inhibition of light emission by 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) and 2,5-dibromo-3-isopropyl-*p*-benzoquinone and the failure of diaminodurol + ascorbate to reverse the inhibition by DCMU. The observation that, with short irradiations (5 µs) no bioluminescence is emitted until the third flash also suggests PSII as the site of stimulation. The evolution of oxygen is not involved in the light-stimulation of bioluminescence, since oxygen evolution is completely inhibited by NH<sub>2</sub>OH, while light emission is potentiated by the presence of NH<sub>2</sub>OH. A consideration of the action of inhibitors suggests that the stimulation of light emission is the result of a change in membrane potential produced upon irradiation of PS II. This membrane potential is not caused by the movement of protons. Maximum fluorescence of dinoflagellates is in the blue-green, 474-478 nm.

Carnegie Institution of Washington, Dept. of Plant Biology, Stanford, CA 94305

193. Tester, P.A. and M.A. Geesey. *Spring bloom 1991, natural phytoplankton assemblages: Can HPLC pigment analyses detect taxa changes?* In *Aquatic Sciences Meeting*, Am. Soc. Limnol. Oceanog., 1992. Santa Fe, NM.

From mid-February to mid-June 1991, two sites (upper and lower Newport estuary) were sampled twice weekly near low tide. Phytoplankton species composition and cell numbers, chlorophyll *a*, and HPLC pigment analyses were determined for each of the 52 samples. Fluctuations in phytoplankton at the shallow, upper estuary site were closely correlated with wind/storm events while the lower estuary was temperature driven. The phytoplankton species composition varied between sites and over the course of the spring bloom and these changes were detectable using HPLC pigment analyses. However, HPLC analyses from the upper estuary site were hindered by detrital resuspension due to wind mixing. In the talk, these authors noted a strong correlation between peridinin and the number

of dinoflagellates, which made up >60% of the algal biomass. Chl *a* was a poor predictor of numbers of dinoflagellates. Diadinoxanthin occurs mostly in dinoflagellates, but also occurs in diatoms.

NOAA, National Marine Fisheries Service, Beaufort, NC 28516

194. Topliss, B.J., *Optical measurements in the Sargasso Sea: solar stimulated chlorophyll fluorescence*. Oceanol. Acta, 1985. 8(3): p. 263-270.

Measurements of total and spectral quantum irradiance were performed at a single location in the Sargasso Sea over a number of days. The spectro-optical characteristics of the water mass were consistent with a relatively high concentration of biogenic material for an oligotrophic ocean station. *In situ*, spectral diffuse attenuation coefficients correlated well with the spectral characteristics of the absorption spectra of particles caught on GF/F filters. The fluorescence signature of chlorophyll *a*, stimulated by the sun, could be detected in all upward irradiance profiles down to depths of 80 m, that is to approximately the 1% of surface light level at 440 nm. Depth variations in the passive chlorophyll fluorescence also correlated with those in both the artificially-stimulated *in vivo* fluorescence and the fluorescence of acetone extracts of filtered samples. The rapid decay with depth of the emission (red) radiation allowed estimates to be made of the fluorescence efficiency at discrete depths throughout the water column. The depth-averaged quantum efficiency of fluorescence was in good agreement with theoretical and laboratory estimates.

Dept. of Fisheries and Oceans, Atlantic Oceanographic Laboratory, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.

195. Topliss, B.J. and T. Platt, *Passive fluorescence and photosynthesis in the ocean; implications for remote sensing*. Deep Sea Res., 1986. 33(7): p. 849-864.

The radiant energy absorbed and fluoresced by phytoplankton can be used to study photosynthesis in the ocean. The efficiency of passive fluorescence by photosynthetic pigments measured at discrete depths in the sea was found to be inversely proportional to the initial slope, *a*, of the photosynthesis-light curve for phytoplankton in the high Arctic and on the Grand Banks. This relationship holds considerable promise as a rapid and non-manipulative method for indexing photosynthesis in both temporal and spatial domains. Potential may also exist to extend the application to large scale, synoptic estimates of surface productivity via remote sensing technology. However, it is neither a simple nor an automatic extension of these studies to consider the surface layer as viewed by remote sensing devices. The blue-green penetration for CZCS type sensors and the red fluorescence penetration for FLI (fluorescence line imager) sensors operate over different physical depths. Dept. of Fisheries and Oceans, Coastal Oceanography, Atlantic Oceanographic Laboratory, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia B2Y 4A2 Canada

196. Topliss, B.J., and T.C. Platt, *The role of passive ocean spectral fluorescence measurements in satellite determinations of marine primary production*. Adv. Space Res., 1987. 7(2): p.107-110.

The detection of spectral fluorescence is a rapidly-growing tool for marine biologists interested in both phytoplankton biomass and species composition. The presence of solar stimulated fluorescence at 685 nm (associated with chlorophyll *a*) has been detected in data sets collected from areas as diverse as the high Arctic and the Caribbean Sea. Interpretation and modeling of passive fluorescence signals in terms of optical efficiencies are dependent on accurate estimates of specific absorption coefficients. This in turn requires an optical modeling of the associated water mass in a similar manner to that used in interpretation of remote sensing signals (such as from the CZCS - Coastal Zone Color Scanner, or the planned OCI - Ocean Colour Imager). A potential relationship between passive chlorophyll fluorescence



efficiency and photosynthetic efficiency of chlorophyll *a* is outlined for the field data and the relevance of such a relationship to future remote sensing signals such as from the FLI (Fluorescence Line Imager) is discussed.

Dept. of Fisheries and Oceans, Atlantic Oceanographic Laboratory, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.

197. Topliss, B.J., *Ocean colour imagery: an investigation of some water-related parameters influencing algorithm development and data product interpretation*. Canadian J. Remote Sensing, 1989. 15(1): p. 56-67.

The objective of this study was to highlight some of the problems remaining in the application and interpretation of ocean colour imagery. This study was illustrated by studying the impact of additional *in situ* ocean parameters on algorithm development and hence on the "look" of a final image product. The water medium was first simulated by a three component water model, which had water, chlorophyll *a*, and detrital material as separate components. Four different water reflectance models were used to simulate optical *in situ* data, which were then compared to each other and to a limited ground truthing data set by using a clear ocean reflectance ratio algorithm of 443 to 550 nm. Factors such as concentration, model type, sampling distribution, proportion of detritus, and scattering functions were all examined for their influence on inferred algorithm coefficients and hence on potential differences between formulae derived in the field. The simulated three component comparisons indicated that if an algorithm was optimised to a high proportion of detrital material, the resulting imagery would underestimate very low proportioned detrital conditions by up to a factor of two. Similarly, an algorithm optimised for a high proportion of chlorophyll *a* would yield imagery that could overestimate high proportioned detrital conditions by up to a factor of three. The illustration of how algorithms and resulting image products were influenced by the addition of a third component was extended to consider coastal influences of suspended sediment and dissolved organic material. At this stage, geographical extension of such algorithms and resulting imagery products was only valid when any additional particulate and dissolved material were oceanographic in origin and present in quantities less than the concentration of chlorophyll-like pigment.

Physical and Chemical Sciences, Dept. of Fisheries and Oceans, Atlantic Oceanographic Laboratory, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, NS, B2Y 4A2, Canada.

198. Venable, D.D., S. Khatun, L. Poole, and A. Punjabi, *Simulated laser fluorosensor from subsurface chlorophyll distributions*. In *Ocean Optics VIII*. 1986. Orlando, FL 637: p. 364-371. SPIE.

A semianalytic Monte Carlo model has been used to simulate laser fluorosensor signals returned from subsurface distributions of chlorophyll. This study assumes the only constituent of the ocean medium is the common coastal zone dinoflagellate *Prorocentrum minimum*. The concentration is represented by Gaussian distributions in which the location of the distribution maximum and the standard deviation are variable. Most of the qualitative features observed in the fluorescence signal for total chlorophyll concentrations up to 1.0 µg/liter can be accounted for with a simple analytic solution assuming a rectangular chlorophyll distribution function.

Dept. of Physics, Hampton University, Hampton, Virginia 23668

199. Voss, K.J. and W. Balch, *Modification of scattering and beam attenuation properties by coccolithophore blooms*. Eos, 1990. 71(2): p. 108.

Coccolithophore blooms in the Gulf of Maine provide an excellent opportunity to measure how the *in-situ* optical properties of the ocean can be modified by a specific

population. During a cruise in the Gulf of Maine, measurements of the spectral phase function using an *in situ* light-scattering instrument and a Bryce-Phoenix light scattering photometer, and the spectral beam attenuation, using a spectral beam transmissometer, were performed. These measurements indicated that the scattering and attenuation characteristics of the water were modified by the presence of these highly scattering phytoplankton. Specifically, both the scattering and the beam attenuation showed a much higher dependence on wavelength than is the case for the ocean in general. The backscatter was found by both instruments to vary by a factor of 2.5 between 550 nm and 450 nm while the particulate beam attenuation varied by a factor of 1.33 at those same wavelengths. These data are contrasted with other spectral measurements of the scattering function and beam attenuation of the coastal Pacific Ocean off of San Diego.

Physics Dept., University of Miami, Coral Gables, Florida 33124 (305 284 2323)

200. Walters, R.A. and R.T. Cheng, *A two-dimensional hydrodynamic model of a tidal estuary*. Advances in Water Resources, 1979. 2(December): p. 177-184.

A finite element model is described which is used in the computation of tidal currents in an estuary. This numerical model is patterned after an existing algorithm and has been carefully tested in rectangular and curve-sided channels with constant and variable depth. One of the common uncertainties in this class of two-dimensional hydrodynamic models is the treatment of the lateral boundary conditions. Special attention is paid specifically to addressing this problem. To maintain continuity within the domain of interest, 'smooth' curve-sided elements must be used at all shoreline boundaries. The present model uses triangular, isoparametric elements with quadratic basis functions for the two velocity components and a linear basis function for water surface elevation. An implicit time integration is used and the model is unconditionally stable. The resultant governing equations are nonlinear owing to the advective and the bottom friction terms and are solved iteratively at each time step by the Newton-Raphson method. Model test runs have been made in the southern portion of San Francisco Bay, California (South Bay) as well as in the Bay west of Carquinez Strait. Owing to the complex bathymetry, the hydrodynamic characteristics of the Bay system are dictated by the generally shallow basins which contain deep, relict river channels. Great care must be exercised to ensure that the conservation equations remain locally as well as globally accurate. Simulations have been made over several representative tidal cycles using this finite element model, and the results compare favourably with existing data. In particular, the standing wave in South Bay and the progressive wave in the northern reach are well represented.

Water Resources Division, U.S. Dept. of Interior, Menlo Park, CA 94025

201. Waters, K.J. and R.C. Smith, *Phytoplankton absorption in ocean waters and the use of optical sensors for the continuous estimate of phytoplankton biomass*. Eos, 1990. 71(2): p. 108.

The absorption of phytoplankton and the influence of changing phytoplankton populations on ocean optical properties are investigated for the purpose of using a nine-month time series of optical data from the Biowatt 1987 deep-sea mooring to study the temporal succession of phytoplankton populations. The absorption due to viable phytoplankton, dissolved organic material, and detrital material are estimated by direct measurement (filter technique) reconstructed pigment spectra and determination of in-water optical properties. The internal consistency of these various absorption estimates is checked by means of Monte Carlo modeling of the natural light field. An optical model is then used to provide a continuous estimate of pigment biomass which shows the successional changes of phytoplankton pigment biomass in response to seasonal forcing.

202. Weaver, E.C. and J.C. Arvesen, *Aerial determination of chlorophyll content in marine and fresh waters*, Eos, 1971. **52**: p. 345.

The productivity of a body of water is correlated with the amount of phytoplankton therein. These photosynthetic microorganisms all contain chlorophyll *a*, a green plant pigment which modifies the spectral composition of the sunlight scattered out of the aquatic environment. A differential radiometer has been constructed and flown in a light aircraft over several types of marine and fresh waters. The instrument makes use of fiber optic bundles to sample incident and upwelled sunlight at several wavelengths. An optical chopper allows continuous comparison of reference and measuring wavelengths so that a signal can be extracted from a high noise background. Measurements are in real time. Direct laboratory measurements of the chlorophyll *a* content have been made on water collected at several depths simultaneously with overflights. A first order relationship between absolute chlorophyll content and the logarithm of optical signal was found to be valid for three orders of magnitude. It is thus possible to have quantitative instantaneous information on a repetitive basis for chlorophyll content in water on a synoptic scale.

Dept. of Biological Sciences, San Jose State University, San Jose, CA 95192

203. Wright, S.W., S.W. Jeffrey, R.F.C. Mantoura, C.A. Llewellyn, J. Bjornlund, D. Repete, N. Welschmeyer. *Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton*. Mar. Ecol. (Prog. Ser.) (in press), 1991.

Using a ternary gradient system, over 50 carotenoids, chlorophylls and their derivatives were separated from marine phytoplankton. Only two pairs of carotenoid pigments and 3 chlorophylls (*c1*, *c2* and Mg 2,4 D) were not resolved. Pigment chromatograms are presented for 12 unialgal cultures from 10 algal classes important in the marine environment. A chromatogram is also given of a complex mixture of over 50 algal pigments such as might be found in a phytoplankton field sample. This method is useful for analysis of phytoplankton pigments in seawater samples and other instances where separations of complex pigment mixtures are required.

Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia

204. Wrigley, R.C., S.A. Klooster, R.S. Freedman, M. Carle, R.E. Slye, and L.F. McGregor, *The Airborne Ocean Color Imager: System description and image processing*. J. of Imaging Technology, 1992. **36**: p. 423-430.

The Airborne Ocean Color Imager (AOCI) was developed as an aircraft instrument to simulate the spectral and radiometric characteristics of the next generation satellite ocean color instrument. Data processing programs have been developed as extensions of the Coastal Zone Color Scanner algorithms for atmospheric correction and bio-optical output products. The latter include several bio-optical algorithms for estimating phytoplankton pigment concentration as well as the diffuse attenuation coefficient of the water. Additional programs have been developed to remap these products into a geo-referenced data base using data from the aircraft's inertial navigation system. Representative data products illustrate sequential steps in the processing using data from flightlines near the mouth of the Mississippi River. The AOCI and its data processing system are being used in several investigations. (Table I lists characteristics of CZCS, AOCI, and SeaWiFS.)

NASA/Ames Research Center, Moffett Field, CA 94035

205. Yentsch, C.S. and C.M. Yentsch, *Fluorescent spectral signatures: The characterization of phytoplankton populations by the use of excitation and emission spectra*. J. Mar. Res., 1979. 37: p. 471-483.

Major groups of algae have quite different excitation spectra for chlorophyll *a* fluorescence emission. Among eucaryotic algae there is considerable difference in the wavelengths of excitation for chlorophyll *a* fluorescence between organisms with a carotenoid-protein complex (diatoms and dinoflagellates) and those without (green algae). In the former, 530 nm is very effective in exciting fluorescence, and not at all effective for green algae. The early trichromatic method of chlorophyll analysis featured the possibility of distinguishing abundance of chloroplastic pigments specific to phyla of algae in the population. The method was not successful however, because in natural populations there are major interferences due to pigments or their degradation products. Much of this can be circumvented using *in vivo* fluorescence techniques. The advantages are that fluorescence from chlorophyll *a* can be excited by wavelengths specific to accessory pigments such as fucoxanthin in diatoms, chromoproteins of the bluegreens and peridinin in the dinoflagellates with only a negligible amount of wavelength overlap. The technique appears to be promising for gross characterization of phytoplankton populations and would be a valuable addition to *in situ* studies where continuous monitoring is employed. The authors comment that "the phytoplankton ecologist should be measuring phycoerythrin as intensely as one does chlorophyll *a*." Also: "Since most imaging satellite sensors are based on the reflectance mode, it does not seem feasible at this time to sense accessory pigmentation from satellites. However, low flying aircraft or helicopters can use the multi-wavelength lasers (pioneered by Mumola *et al.*, 1975) and thus can be a valuable addition to remote sensing characterization." Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, Maine 04575

206. Yentsch, C.S., *Light attenuation and phytoplankton photosynthesis*, in *The Physiological Ecology of Phytoplankton*, I. Morris, Editor. 1980, University of California Press: Berkeley and Los Angeles. p. 95-127.

Sections: Introduction, General scheme for the partitioning of light in the oceans, Factors which attenuate light in the oceans, (Competition between water and photosynthetic pigments, The attenuation of light by phytoplankton, Spectral absorption by phytoplankton and particulate matter, Absorption of dissolved yellow substances); The action of light in photosynthesis in natural populations (Fluorescence spectra - excitation and emission, Fluorescence-chlorophyll relationships, Photosynthesis vs. light intensity, Measurement of photosynthetic light); Remote sensing; Final comments; References.  
Bigelow Laboratory for Ocean Sciences, McKown Point, West Boothbay Harbor, Maine, 04575, USA

207. Yentsch, C., D.A. Phinney, and L. Shapiro. *Absorption and fluorescent characteristics of the brown tide chrysophyte: its role in light reduction in coastal marine environments*. in *Novel Phytoplankton Blooms: Causes and Impact of Recurrent Brown Tides and Other Unusual Blooms*. Cosper *et al.*, eds. 1988. SUNY, Stonybrook, NY: Springer-Verlag.

Novel phytoplankton blooms, in particular those detrimental to coastal marine resources, can be conveniently placed into two broad categories. One is where toxic substances produced by the alga detrimentally affect the other species' growth or aspects of metabolism of other species. The other is where the sheer magnitude of the bloom changes environmental conditions which leads to the demise of other species. Alternatively, the brown tide organism (*Aureococcus*) may have unique absorption characteristics caused by photosynthetic pigments, which could reduce water transparency and thus affect the light environment for other species. We found that this brown tide organism selectively absorbs blue light and markedly changes the submarine light field. If these spectra are unique, there

exists the possibility to use the unique features in a scheme for remote sensing. One possibility is to use the fluorescence excitation spectra, with the ratio of 530 nm/450 nm giving an indication of the type of organisms present, since the brown tide chrysophyte has a much higher peak in the blue than the diatom (*Skeletonema*) used for comparison. Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, ME 04675

208. Yentsch, C.S. and D.A. Phinney. *Relationship between cross-sectional absorption and chlorophyll content in natural populations of marine phytoplankton*. in *Ocean Optics IX*. 1988. Orlando, FL 925: p. 109-112. SPIE.

We have measured the *in vivo* absorption of light (670 nm) by natural phytoplankton populations collected from a variety of locations in the North Atlantic Ocean. There is a strong correlation between chlorophyll content and absorption. By using a linear regression model the mean value for chlorophyll specific absorption ( $A^*$ ) is 0.0138. The range in this value is about 0.0100-0.0300. At chlorophyll concentrations less than 0.5  $\mu\text{g/l}$  the slope differs from the slope at higher concentrations. The scatter of points around the mean increases with increasing chlorophyll. By grouping chlorophyll concentrations a mean and standard error have been determined for each group. This allows the entire data set to be fitted with a power model curve ( $Y=aX^b$ ). The exponent  $b$  is 0.758 (3/4) which argues that  $A^*$  is a function of cell volume,  $A^*=0.0667\text{Chl}^{0.758}$  where Chl is in  $\mu\text{g/l}$ . Bigelow Laboratory for Ocean Sciences, McKown Point, West Boothbay Harbor, Maine 04575.

209. Yentsch, C.S. and D.A. Phinney. *Autofluorescence and Raman scattering in the marine underwater environment*. in *Ocean Optics X*. 1990. Orlando, FL 1302: p. 328-333. SPIE.

The predictive effects of Raman scattering on the inherent optical characteristics of aquatic water masses raises questions concerning our ability to estimate how light energy is budgeted. Using values for the optical cross-section of water and biogenic substances, we estimate the relative contribution of fluorescence from the Raman scattering to the underwater radiance field. We conclude that in oligotrophic water fluorescence overwhelms Raman scattering. (Note: This paper contains a spectrum for phycoerythrin fluorescence, from cryptomonads.)

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13. ABSTRACT (Maximum 200 words)  A literature review was conducted of the state of the art as to whether or not information about communities and populations of phytoplankton in aquatic environments can be derived by remote sensing. In order to arrive at this goal, the spectral characteristics of various types of phytoplankton were compared to determine first, whether there are characteristic differences in pigmentation among the types and second, whether such differences can be detected remotely. In addition to the literature review, an extensive, but not exhaustive, annotated bibliography of the literature that bears on these questions is included as an appendix since it constitutes a convenient resource for anyone wishing an overview of the field of ocean color.  The review found some progress has already been made in remote sensing of assemblages such as coccolithophorid blooms, mats of cyanobacteria, and red tides. Much more information about the composition of algal groups is potentially available by remote sensing particularly in water bodies having higher phytoplankton concentrations, but it will be necessary to develop the remote sensing techniques required for working in so-called Case 2 waters. It is also clear that none of the satellite sensors presently available or soon to be launched is ideal from the point of view of what we might wish to know; it would seem wise to pursue instruments with the planned characteristics of the Moderate Resolution Imaging Spectrometer-Tilt (MODIS-T) or Medium Resolution Imaging Spectrometer (MERIS).				
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